

# Atmospheric feedbacks reverse the sensitivity of modeled photosynthesis to stomatal function

Amy X. Liu<sup>1</sup>, Claire M. Zarakas<sup>1</sup>, Benjamin G. Buchovecky<sup>1</sup>, Linnia R. Hawkins<sup>2</sup>, Alana S. Cordak<sup>3</sup>, Ashley E. Cornish<sup>3</sup>, Marja Haagsma<sup>4</sup>, Gabriel J. Kooperman<sup>3</sup>, Chris J. Still<sup>5</sup>, Charles D. Koven<sup>6</sup>, Alexander J. Turner<sup>1</sup>, David S. Battisti<sup>1</sup>, James T. Randerson<sup>7</sup>, Forrest M. Hoffman<sup>8</sup>, Abigail L.S. Swann<sup>1,9</sup>

<sup>1</sup>University of Washington, Seattle, Department of Atmospheric and Climate Science

<sup>2</sup>Columbia University, Department of Earth and Environmental Engineering

<sup>3</sup>University of Georgia, Department of Geography

<sup>4</sup>Oregon State University, Department of Biological and Ecological Engineering

<sup>5</sup>Oregon State University, Department of Forest Ecosystems and Society

<sup>6</sup>Lawrence Berkeley National Laboratory, Climate and Ecosystem Sciences Division

<sup>7</sup>University of California, Irvine, Department of Earth System Science

<sup>8</sup>Oak Ridge National Laboratory

<sup>9</sup>University of Washington, Seattle, Department of Biology

## Key Points:

- Atmospheric feedbacks reverse the direction of photosynthesis sensitivity to stomatal function in the tropics and high latitudes
- Stomatal function with higher water cost per carbon gain leads to substantially reduced photosynthesis, especially in the tropics
- The inclusion of atmospheric feedbacks is critical for evaluating stomatal function in land surface models

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Corresponding author: Amy X. Liu, amyxliu@uw.edu

## Abstract

Stomata mediate fluxes of carbon and water between terrestrial plants and the atmosphere. These fluxes are governed by stomatal function and can be modulated in many Earth system models by an empirical parameter within the calculation of stomatal conductance, the stomatal slope ( $g_{1M}$ ). Intuitively,  $g_{1M}$  represents the marginal water cost of carbon, relating it to the emergent plant property of water use efficiency. Observations show that  $g_{1M}$  can range widely across and within plant types in varying environments, and this distribution of  $g_{1M}$  is not captured within Earth system models which represent each plant type with a single  $g_{1M}$  value. Here we examine how  $g_{1M}$  influences photosynthesis using coupled Earth system model simulations by perturbing  $g_{1M}$  to observed 5<sup>th</sup> and 95<sup>th</sup> percentiles for each plant type. We find that high  $g_{1M}$  reduces photosynthesis nearly everywhere, while low  $g_{1M}$  has regionally dependent responses. Under fixed atmospheric conditions, low  $g_{1M}$  increases photosynthesis in the Amazon and central North America but decreases photosynthesis in boreal Canada. These responses reverse when the atmosphere responds interactively due to spatially differing sensitivity to increases in temperature and vapor pressure deficit. Choice of  $g_{1M}$  also influences photosynthetic response to changes in atmospheric carbon dioxide ( $\text{CO}_2$ ), with lower and higher  $g_{1M}$  modifying total global response to elevated 2x preindustrial  $\text{CO}_2$  by 6.4% and -9.6%, respectively. Our work demonstrates that atmospheric feedbacks are critical for determining the photosynthetic response to  $g_{1M}$  assumptions and some regions are particularly sensitive to choice of  $g_{1M}$ .

## Plain Language Summary

Plants affect the Earth system’s carbon, water, and energy fluxes through photosynthesis and transpiration, regulated by stomata that control gas exchange. Stomatal function controls the water cost per carbon gain for photosynthesis, where lower water cost means less water lost per carbon gain and higher water cost means more water lost. Observations show a range of stomatal function across and within plant types in varying environments which are not captured in Earth system models. In our study, we explored how changes in stomatal function impact photosynthesis using an Earth system model. We find higher water cost generally decreases photosynthesis everywhere while lower water cost has mixed effects, increasing photosynthesis in the Amazon and central North America but decreasing it in boreal Canada. These responses change when we allow the atmosphere to respond to changes on land, mainly due to spatially varying sensitivity to warmer temperature and drier air. Additionally, changes in stomatal function alter photosynthetic response to higher atmospheric carbon dioxide concentrations, with lower and higher water cost changing global photosynthesis by 6.4% and -9.6%, respectively. Our study demonstrates that accounting for atmospheric responses to land changes is critical for understanding the sensitivity of photosynthesis to stomatal function.

## 1 Introduction

Stomatal functioning mediates water loss through transpiration and carbon gain through photosynthesis, influencing the water and carbon fluxes between plants and the atmosphere (G. B. Bonan, 2008). A change in stomatal function shifts how stomata physiologically regulates the gas exchange, altering conductance of atmospheric carbon dioxide ( $\text{CO}_2$ ) for photosynthesis and water vapor for transpiration.

The theory for optimal stomatal behavior suggests that plants dynamically adjust their stomatal opening (and thus conductance) to achieve a balance between the rate of photosynthesis and water loss from transpiration, resulting in an “optimal” relationship that can be expressed mathematically (Cowan & Farquhar, 1977; Arneeth et al., 2002). Empirical formulations for stomatal conductance are derived using observations of stom-

atal behavior under different environmental conditions including atmospheric dryness, temperature, and atmospheric CO<sub>2</sub> concentration (Ball et al., 1987; Leuning, 1995). Medlyn et al. (2011) developed a unified formulation for stomatal conductance, based off the optimal theory and expressed in empirical form, yielding physiologically meaningful parameters that can be estimated from data. Regardless of the approach taken to represent stomatal behavior under different environmental conditions, more open stomata tend to increase both transpiration and the uptake of carbon for photosynthesis, and vice-versa for more closed stomata. As a result, stomatal conductance, photosynthesis and transpiration are tightly coupled under most conditions, though they can become decoupled under high temperature conditions (De Kauwe et al., 2019). Stomatal function governs the ratio of these processes, or the marginal water cost of carbon gain.

### 1.1 Uncertainty in $g_{1M}$

In common process-based models that explicitly represent photosynthesis rates and stomatal conductance (e.g., Farquhar, Caemmerer, & Berry, 1980, Ball et al., 1987, Leuning, 1995, Medlyn et al., 2011), stomatal function can be modified by one of the empirically fit parameters. We will focus here on the Medlyn et al. (2011) formulation of stomatal conductance,  $g_s$ , given by

$$g_s = g_0 + 1.6(1 + \frac{g_{1M}}{\sqrt{VPD}}) \frac{A_n}{c_s}, \quad (1)$$

where  $A_n$  is photosynthesis,  $c_s$  is the atmospheric CO<sub>2</sub> concentration, VPD is vapor pressure deficit, and  $g_0$  is the Medlyn intercept (minimum stomatal conductance, when the stomata are completely closed).  $A_n$  is coupled to  $g_s$ , and an increase in stomatal conductance relates to an increase in photosynthesis. The stomatal slope,  $g_{1M}$ , is an empirically estimated parameter that is determined by the marginal water cost of carbon gain and related to the emergent plant property of intrinsic water use efficiency (iWUE; Medlyn et al., 2011).

Observationally-based estimates of  $g_{1M}$  exist for only a small subset of climatic space represented on Earth. Even in this limited climate space,  $g_{1M}$  shows a large variation both across plant types and within a plant type (Lin et al., 2015; Wolz et al., 2017; Y. Liu et al., 2021). However, in many land surface models, including those within Earth system models, for tractability a single  $g_{1M}$  value is assigned to each plant type, even though the plant type may exist in many locations with different climates. In the land surface component of the Community Earth System Model version 2 (CESM2), the average  $g_{1M}$  within a grid cell has variation (Fig. 1a) since there are fourteen different plant functional types (PFTs), and each PFT has its own distribution and a different  $g_{1M}$  derived from Lin et al. (2015). Given that there is a large observed range in the value of  $g_{1M}$  for each plant type (e.g., Lin et al., 2015), the actual distribution of average  $g_{1M}$ , and thus stomatal function, is also uncertain.

Photosynthesis is expected to increase while  $g_s$  is expected to decrease in response to elevated atmospheric CO<sub>2</sub> (Adams et al., 2020; Li et al., 2023). Under elevated CO<sub>2</sub>, CO<sub>2</sub> diffuses more easily into leaves, prompting plants to alter their stomatal functioning to optimize carbon gain to water loss, which could lead to either further increases in photosynthesis or reductions in transpiration per leaf area (Keenan et al., 2013; Frank et al., 2015). Additionally, more photosynthesis can lead to increases in leaf area, which could increase total photosynthesis and transpiration (Field et al., 1995).

To evaluate the role of stomatal functioning, we investigate the sensitivity of photosynthesis to different assumptions about  $g_{1M}$  in an Earth system model under both historical and future climate conditions. Intuitively, low  $g_{1M}$  corresponds to less water loss per unit carbon gain (low water cost) and high  $g_{1M}$  corresponds to more water loss per carbon gain (high water cost). We examine two research questions: first, what are the mechanisms and feedbacks through which different assumptions about  $g_{1M}$  impact

photosynthesis and how do they vary spatially (Section 3.2); and second, what is the impact of uncertainty in  $g_{1M}$  on the response of photosynthesis to elevated atmospheric  $\text{CO}_2$  concentrations (Section 3.3)? We focus our analysis on the response of photosynthesis as it integrates the response of both carbon and water cycling to assumptions about stomatal function, with  $g_{1M}$  serving as a metric to quantify these variations.

## 2 Methods

### 2.1 Model configurations

We used the Community Earth System Model version 2 (CESM2; Danabasoglu et al., 2020), an open-source Earth system model, to estimate the response of photosynthesis to different assumptions of  $g_{1M}$ . CESM2 is comprised of the Community Land Model 5 (CLM5; D. M. Lawrence et al., 2019), the Community Atmosphere Model 6 (CAM6; Bogenschutz et al., 2018), and a slab ocean based on output from the CESM2 Coupled Model Intercomparison Project Phase 6 (CMIP6) preindustrial control run (Danabasoglu & Gent, 2009). We performed global-scale simulations of CESM2 at  $0.9 \times 1.25^\circ$  spatial resolution.

In order to isolate the impacts of atmospheric response and dynamic leaf area to different values of  $g_{1M}$ , we defined two configurations of CESM2. The “Land-Atmosphere” configuration (LndAtm) was run with a dynamic atmosphere and a land model that included active biogeochemistry and prognostic leaf area that allowed for leaf area to dynamically respond to climate, resulting in changes in both atmospheric conditions and leaf area in response to  $g_{1M}$  (water cost) perturbations. The active biogeochemistry component tracks both carbon and nitrogen using vertically resolved carbon pools and representation of nitrogen cycling (D. M. Lawrence et al., 2019). The “Land-Only-Fixed-Leaf” configuration (LndOnly) is the same land model but with the leaf area phenology specified as a repeating seasonal cycle of climatological leaf area, so there were no changes in both atmospheric conditions and year-to-year leaf area in response to  $g_{1M}$  perturbations. The Land-Only-Fixed-Leaf simulations are used as a counterfactual to understand the changes in stomatal function, photosynthesis, and climate in the Land-Atmosphere preindustrial  $\text{CO}_2$  simulations.

In order to compare the response of atmospheric feedbacks and prognostic leaf area under equivalent meteorological conditions, we prescribed the meteorological forcing in the Land-Only-Fixed-Leaf simulations using the output of the default  $g_{1M}$  Land-Atmosphere simulation saved at 3 hourly intervals. The 3-hourly meteorological data is interpolated to 30 minute time resolution to drive the Land-Only-Fixed-Leaf simulations. We analyzed the last 80 years of a 120-year simulation, after discarding the first 40 years to allow the system to reach equilibrium.

Broadly in CLM5,  $g_s$  and photosynthesis are calculated iteratively from environmental conditions estimated at the leaf level, including air temperature, vapor pressure deficit (VPD), atmospheric  $\text{CO}_2$  concentration, and photon flux density using  $g_s$  formulated as in Medlyn et al. (2011) (Equation 1), and photosynthesis from Farquhar, Caemmerer, and Berry (1980), G. J. Collatz, Ball, Grivet, and Berry (1991), and G. Collatz, Ribas-Carbo, and Berry (1992). Total canopy latent heat fluxes are altered by  $g_s$ , leaf area, leaf boundary layers and aerodynamic resistance. More details can be found in the CLM5 technical note in Section 2.5.3 and 2.9 (D. Lawrence et al., 2018).

CLM5 with default parameters represents photosynthesis well relative to other land models in the International Land Model Benchmarking (ILAMB) in an integrated assessment (e.g., biases, spatial patterns, etc.) against observational datasets, and its global photosynthesis (119 Pg C/year) is similar to that of FLUXNET-MTE (118 Pg C/year) (D. M. Lawrence et al., 2019). Regionally, CLM5 captures the spatial and seasonal patterns of photosynthesis in contiguous United States when compared to FLUXNET-MTE,



**Table 1.** Summary of Simulations.

Group	Simulation Name	CO <sub>2</sub>	Atmosphere	Leaf Area	$g_{1M}$ (Water Cost)
<b>LndAtm</b>	Land-Atmosphere low $g_{1M}$	1xCO <sub>2</sub>	dynamic	prognostic	low
	Land-Atmosphere default $g_{1M}$				default
	Land-Atmosphere high $g_{1M}$				high
<b>LndOnly</b>	Land-Only-Fixed-Leaf low $g_{1M}$	1xCO <sub>2</sub>	prescribed	prescribed	low
	Land-Only-Fixed-Leaf default $g_{1M}$				default
	Land-Only-Fixed-Leaf high $g_{1M}$				high
<b>LndAtm2x</b>	Land-Atmosphere 2xCO <sub>2</sub> low $g_{1M}$	2xCO <sub>2</sub>	dynamic	prognostic	low
	Land-Atmosphere 2xCO <sub>2</sub> default $g_{1M}$				default
	Land-Atmosphere 2xCO <sub>2</sub> high $g_{1M}$				high

The sensitivity to  $g_{1M}$  is calculated by comparing simulations within an experiment group (e.g., LndAtm low  $g_{1M}$  minus LndAtm default  $g_{1M}$ ; Section 2.3.1). The effect of atmospheric and leaf area feedbacks is calculated by comparing experiment groups LndAtm and LndOnly (Section 2.3.2). The total response to elevated CO<sub>2</sub> is calculated by taking experiment group LndAtm2x minus group LndAtm (Section 2.3.3).

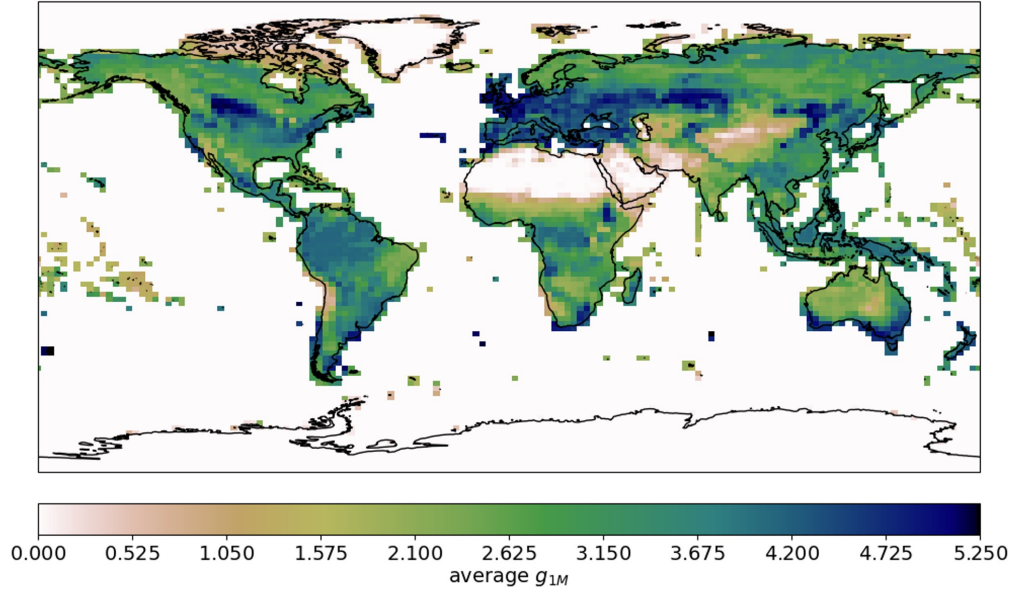
though photosynthesis is underestimated during the growing season (Cheng et al., 2021). These assessments mainly focus on simulations with prescribed atmospheric forcing, but CESM2 simulations with atmospheric feedbacks also perform relatively well for photosynthesis against other Earth system models (D. M. Lawrence et al., 2019).

## 2.2 $g_{1M}$ Perturbations

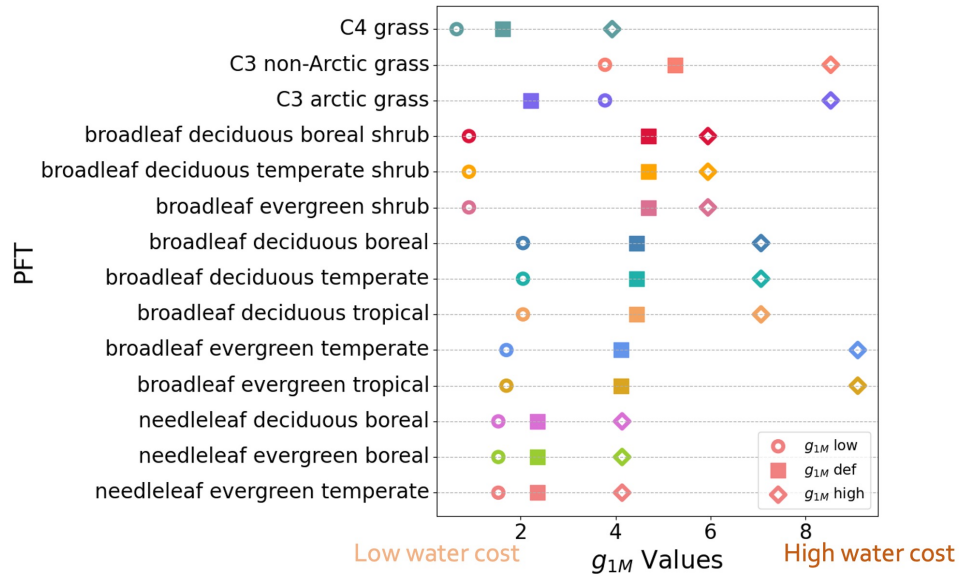
We investigate the response of photosynthesis to assumptions about plant stomatal function by perturbing the stomatal slope parameter,  $g_{1M}$ , within Equation 1. These perturbations reflect variations in stomatal function, as  $g_{1M}$  is related to the marginal water cost of carbon (Medlyn et al., 2011). To add intuition, we additionally describe our results in terms of the change in water cost associated with a perturbed  $g_{1M}$ , where high  $g_{1M}$  represents a higher cost of water and vice versa. This intuition is consistent with measurements of  $g_{1M}$  across FLUXNET stations, where drier stations tend to show lower  $g_{1M}$  and more water use efficient behavior while stations in wetter regions tend to show higher  $g_{1M}$  and less water use efficient behavior (Lin et al., 2015; De Kauwe et al., 2015; Knauer et al., 2015). We perturbed  $g_{1M}$  to a minimum and maximum for each PFT based on the 5<sup>th</sup> and 95<sup>th</sup> percentile from observations (Lin et al., 2015; Fig. 1b), such that we have one set of simulations that use the 5<sup>th</sup> percentile values for  $g_{1M}$  (“low  $g_{1M}$ ” or “low water cost”) and one set of simulations that use 95<sup>th</sup> percentile values for  $g_{1M}$  (“high  $g_{1M}$ ” or “high water cost”). The range of  $g_{1M}$  across PFTs from the leaf-level estimates used in our study is similar to the range derived from isotopic measurements and FLUXNET observations (Medlyn et al., 2017).

We quantify the effect of a change in  $g_{1M}$  by comparing the low or high  $g_{1M}$  simulations against simulations with the default  $g_{1M}$  parameter values used in CLM5, noting that these default values do not represent the mean or median of the range of observations we used for perturbation (Fig. 1b). The average  $g_{1M}$  for any given grid cell is a weighted average that varies due to the distribution of PFTs within the grid cell and the range of default  $g_{1M}$  values across PFTs (Fig. 1a).

(a) Distribution of Default  $g_{1M}$  values



(b) Low, Default, and High  $g_{1M}$  values for each PFT



**Figure 1.** (a) Spatial plot of default PFT-area-weighted  $g_{1M}$  values used in CLM5. (b) Plot of the default and perturbed stomatal slope parameter,  $g_{1M}$ , for each vegetation type in the CLM5.

## 2.3 Simulation design

In order to isolate the effects of multiple processes that comprise the full climate and ecosystem response to stomatal function, we performed nine simulations (Table 1). For each simulation we set  $g_{1M}$  (water cost) to either default, low, or high values which intuitively corresponds to default, low, or high water cost per carbon gain. We tested two configurations of CESM2, one with atmosphere and prognostic leaf area components working interactively (“Land-Atmosphere”; experimental group “LndAtm” in Table 1), and one where both meteorological forcing and leaf area phenology are prescribed (“Land-Only-Fixed-Leaf”; experimental group “LndOnly” in Table 1). Both configurations were run at preindustrial atmospheric  $\text{CO}_2$  concentrations (284.7 ppm) and the Land-Atmosphere configuration was additionally run with 2x preindustrial atmospheric  $\text{CO}_2$  concentrations (569.4 ppm; experimental group “LndAtm2x” in Table 1) in order to assess the sensitivity of climate and photosynthesis to uncertainty in  $g_{1M}$  under elevated  $\text{CO}_2$  concentrations. Going forward, we refer to simulations by their experimental group names (e.g., LndAtm, LndOnly, and LndAtm2x) for readability in the text, while figures and tables use the full simulation name (e.g., Land-Atmosphere low  $g_{1M}$  and Land-Only-Fixed-Leaf low  $g_{1M}$ ).

### 2.3.1 Quantifying impact of perturbations in $g_{1M}$

We implement perturbations to the  $g_{1M}$  parameter as described above, resulting in simulations with lower or higher  $g_{1M}$  (water cost) relative to the default in CLM5. To quantify a photosynthesis or climate response to a change in  $g_{1M}$ , we calculated the response of a variable by comparing the simulations with either low or high  $g_{1M}$  against the simulations with default  $g_{1M}$  (comparison within an experiment group in Table 1). We averaged across all 80 post-spinup years to quantify the equilibrium response to a  $g_{1M}$  perturbation. We report both the actual difference between simulations and percentage difference between simulations for individual variables. Unless otherwise noted, percentage difference for a variable was calculated by taking the relative difference of that variable between two simulations and dividing it by the time average in the default  $g_{1M}$  simulation. The focus of our analysis is on annual photosynthesis. Generally, the response of annually averaged photosynthesis is similar to that averaged over from the growing season only, and so we report the annual averages here.

### 2.3.2 Quantifying impact of dynamic atmosphere and prognostic leaf area

To understand how the combined atmospheric and leaf area feedbacks modify the climate impact of  $g_{1M}$  (water cost), we compared the response of a variable to a  $g_{1M}$  perturbation between experimental groups LndAtm and LndOnly (Table 1). For example, we compared the difference between the low and default  $g_{1M}$  simulations within LndOnly with the difference between the low and default  $g_{1M}$  simulations within LndAtm. In addition to calculating the absolute difference we also compared just the change in sign of photosynthetic response by filtering for grid cells with a sign change in photosynthetic response to  $g_{1M}$  perturbation between LndOnly and LndAtm.

### 2.3.3 Quantifying impact of elevated atmospheric $\text{CO}_2$

We performed two comparisons with the 2x $\text{CO}_2$  simulations. First, we quantified the absolute response of a variable to an increase in atmospheric  $\text{CO}_2$  by comparing 2x $\text{CO}_2$  simulations to their parallel configuration 1x $\text{CO}_2$  simulations, e.g., LndAtm2x low  $g_{1M}$  - LndAtm low  $g_{1M}$  (Table 1). Second, we quantified how the response of a variable to elevated  $\text{CO}_2$  changes with  $g_{1M}$ . We did this by comparing the response to elevated  $\text{CO}_2$  across different  $g_{1M}$  values, e.g., (LndAtm2x low  $g_{1M}$  - LndAtm  $g_{1M}$ ) - (LndAtm2x de-

fault  $g_{1M}$  - LndAtm  $g_{1M}$ ), which allowed us to remove the effect of elevated  $\text{CO}_2$  and look at how changes in  $g_{1M}$  modify the response.

#### 2.3.4 Regional analysis

In addition to global climate response to perturbations in  $g_{1M}$  (water cost), we focused on the response in three regions, each spanning different background climates: the tropical forest Amazon (13°S to 5°S and 68°W to 57°W), the temperate grassland central North America (central NA; 40°N to 52°N and 103°W to 96°W), and boreal forest Canada (50°N to 57°N and 78°W to 69°W). We calculated the regional climate response by taking the area-weighted average across all of the grid cells in each region.

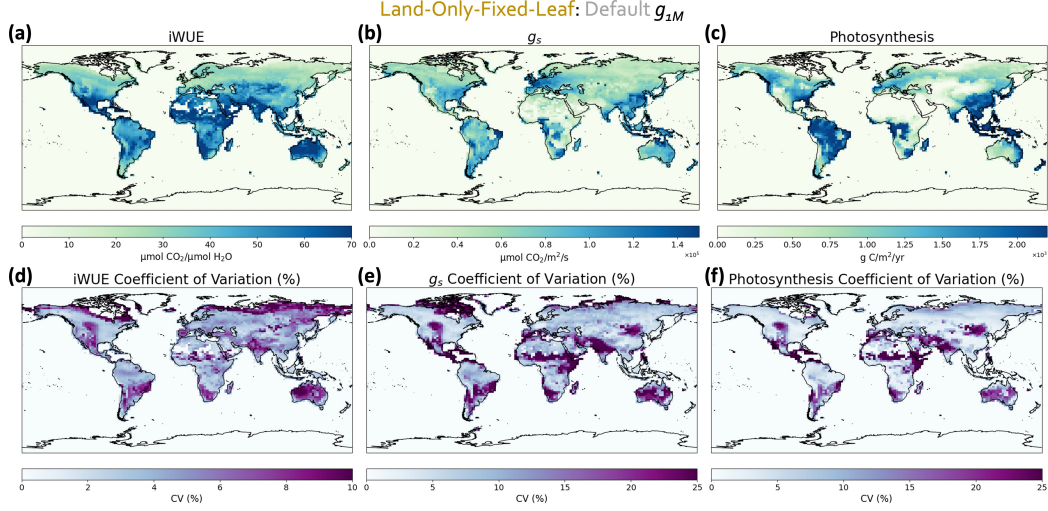
### 2.4 Perturbed meteorology simulations

In addition to comparing our different  $g_{1M}$  (water cost) simulations, we used an additional set of simulations to directly isolate the effects of temperature and vapor pressure deficit (VPD) on photosynthesis and aid in the interpretation of our results from the perturbed  $g_{1M}$  simulations. These are sensitivity experiments, intended to isolate the effect of individual climate factors. We refer to these simulations as “perturbed meteorology” simulations. In each simulation, a single meteorological variable was modified in a version of the model with a prescribed atmosphere and prognostic leaf area at default  $g_{1M}$  configuration. We completed two perturbed meteorology simulations. The first isolates the effects of temperature by increasing the bottom-of-atmosphere temperature in each grid cell by 1°C, while keeping the specific humidity constant. VPD is calculated based on the the bottom-of-atmosphere temperature, pressure, and specific humidity, so it is an indirect effect of temperature. Thus the temperature perturbed simulation accounts for both the indirect and direct effects of temperature on photosynthesis. The second simulation isolated the effects of VPD by imposing a 10% increase in the bottom-of-atmosphere specific humidity in each grid cell, while keeping the temperature constant. This allows us to isolate the effects of VPD on photosynthesis that are not driven by changes in temperature. Details on how we calculated the expected response of photosynthesis to temperature and VPD changes from  $g_{1M}$  perturbations can be found in Supplemental Text S1.

### 2.5 Statistical significance

We used a test of statistical significance to determine if annually-averaged responses in the perturbed  $g_{1M}$  (water cost) simulations differed from those in the default  $g_{1M}$  simulation. We report our results as statistically significant when a two-tailed student’s t-test with an assumed 40 degrees of freedom has a p-value that passes the false discovery rate of 0.05. We use a conservative estimate for degrees of freedom that assumes variables exhibit an auto-correlation of less than two years. The false discovery rate, or the fraction of false positives, is important in our analysis because we perform a t-test at many grid cells and accounting for it makes our p-values more conservative (Wilks, 2016). In the spatial maps, grid cells that do not pass the statistical test are indicated with stippling.

For simple comparisons between two simulations (e.g., LndAtm low  $g_{1M}$  - LndAtm default  $g_{1M}$ ), we compare their output distributions with the null hypothesis that there is no statistical difference between them. For comparisons of responses between simulations (e.g., (LndAtm low  $g_{1M}$  - LndAtm  $g_{1M}$ ) and (LndOnly low  $g_{1M}$  - LndOnly default  $g_{1M}$ )), we use bootstrapping (n=1000) to generate empirical distributions of the responses and test for significance. Since simulation years are samples of a climate-state rather than aligned in time, we assess statistical significance through bootstrapped distributions rather than direct year-to-year comparison.



**Figure 2.** Spatial plots of Land-Only-Fixed-Leaf (LndOnly) default  $g_{1M}$  (water cost) simulations showing the mean of (a) iWUE, (b)  $g_s$ , and (c) photosynthesis. (d-f) show the corresponding coefficient of variation (standard deviation divided by the mean) for iWUE,  $g_s$ , and photosynthesis.

### 3 Results

#### 3.1 Intrinsic water use efficiency at default $g_{1M}$

Plant intrinsic water use efficiency (iWUE) is the ratio of the rate of carbon gain to the rate of water loss; it is an emergent property that results from the coupled behavior of photosynthesis and  $g_s$ . In the LndOnly default  $g_{1M}$  simulation, the most simple simulation with no atmospheric and leaf area feedbacks, iWUE has a global mean of 41.29  $\mu\text{molCO}_2/\mu\text{molH}_2\text{O}$ ,  $g_s$  has a global mean of just under 60,000  $\mu\text{molCO}_2/\text{m}^2/\text{s}$ , and photosynthesis has a global mean of 853.41  $\text{gC}/\text{m}^2/\text{year}$ . Spatially, iWUE is higher in lower latitudes,  $g_s$  is higher in regions such as South America, Central and Eastern North America, Europe, Eastern China, Southeast Asia, and Australia, while photosynthesis tends to be higher in the tropics (cf. Fig. 2a-c). All three share a similar spatial pattern of coefficient of variation (the magnitude of the standard deviation relative to the mean; cf. Fig. 2d-f), which is expected given their coupled relationship.

In the LndOnly simulations, a high  $g_{1M}$  perturbation increases the global average  $g_s$ , or diffusion of  $\text{CO}_2$  into leaf, by around 41,700  $\mu\text{molCO}_2/\text{m}^2/\text{s}$  (+70.3%) from default  $g_{1M}$  and low  $g_{1M}$  perturbation decreases global average  $g_s$  by just over 20,000  $\mu\text{molCO}_2/\text{m}^2/\text{s}$  (-33.9%). The inclusion of atmospheric and leaf area feedbacks in the LndAtm simulations yields a similar magnitude of  $g_s$  response and an amplified iWUE response compared to those in the LndOnly simulations (cf. Figs. S1-4a&b). This suggests that changes in iWUE are mainly driven by changes in photosynthesis.

#### 3.2 Photosynthetic response to $g_{1M}$

Total global photosynthesis in the LndAtm simulations varied across our  $g_{1M}$  (water cost) perturbations, with 120 PgC/year in the default  $g_{1M}$ , 99 PgC/year in the high  $g_{1M}$ , and 112 PgC/year in the low  $g_{1M}$ . Below we describe the causes for changes in photosynthesis associated with each  $g_{1M}$  perturbation in more detail.



### 3.2.1 Impacts of high $g_{1M}$

In the LndAtm high  $g_{1M}$  (high water cost) simulation, photosynthesis decreased across the globe (Fig. 3b) relative to the default  $g_{1M}$  simulation by  $138 \text{ gC/m}^2/\text{year}$ . There were larger absolute decreases in photosynthesis near the equator, due to greater overall plant productivity in the tropics. Modeled photosynthesis decreased with higher  $g_{1M}$  because plants open their stomata and transpire more (Figs. S2b&c) leading to a cascade of changes to other variables that affect photosynthesis. Greater transpiration rates deplete plant and soil water supply making plants more soil water stressed (Fig. S2d), leading to a decrease in the number of leaves that a plant can support (Fig. S2g) which decreased total photosynthesis (Fig. 3b). VPD decreased along with decreases in surface temperature due to greater transpiration, which decreased atmospheric water stress. One might have expected the decrease in VPD to alleviate overall plant water stress, however the increase in soil water stress was greater than the decrease in atmospheric water stress with higher  $g_{1M}$  which accounts for the decrease in photosynthesis in our simulations.

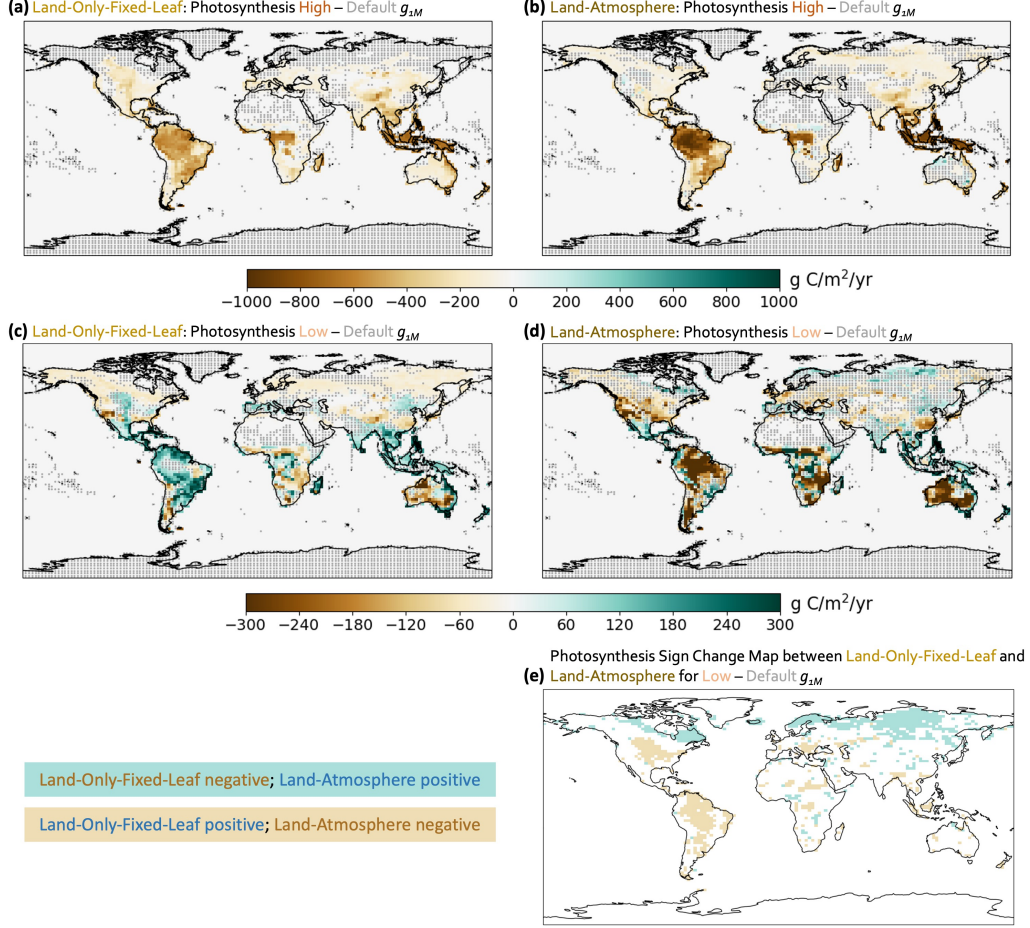
The photosynthetic response to higher  $g_{1M}$  was similar with and without dynamic atmosphere and prognostic leaf area (cf. Figs. 3a&b). Both configurations showed decreases in photosynthesis across the globe in response to higher  $g_{1M}$  with similar spatial patterns but with a larger magnitude of change in the LndAtm high  $g_{1M}$  simulation driven largely by leaf area decreases (Fig. S2g) that are precluded in the LndOnly high  $g_{1M}$  simulation.

### 3.2.2 Impacts of low $g_{1M}$

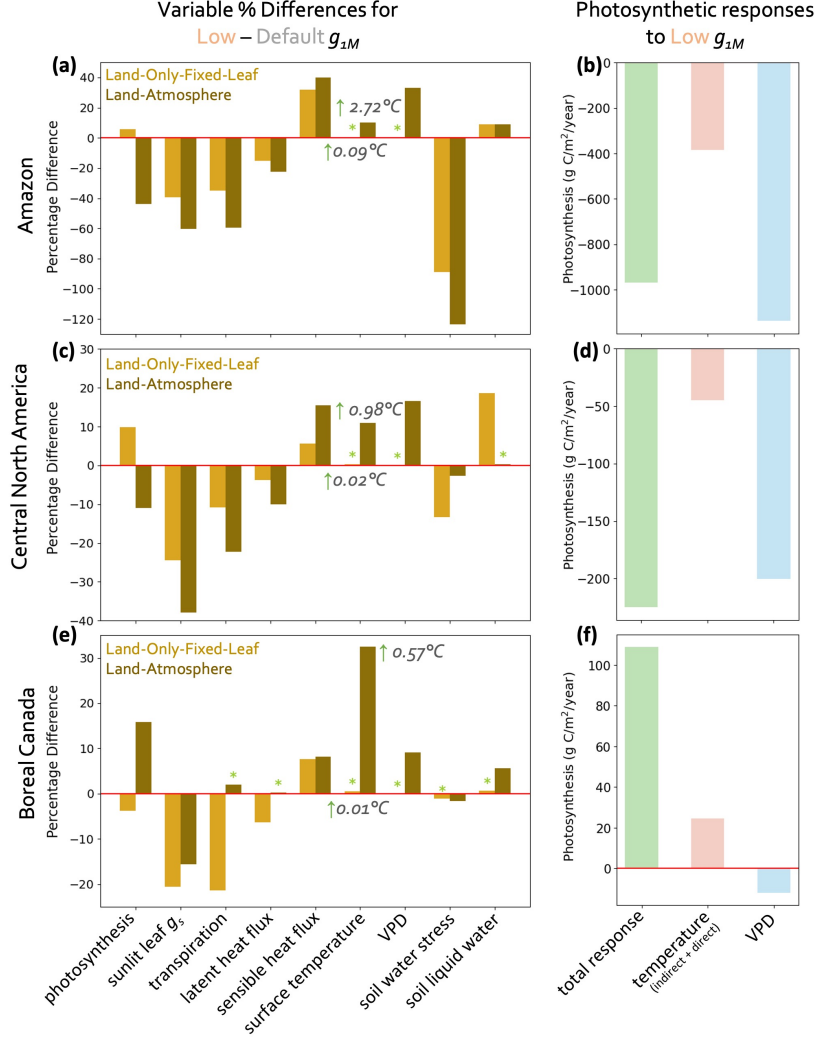
Given that higher water cost led to lower photosynthesis due to soil water stress, our naive expectation is that lower water cost should lead to higher rates of photosynthesis. However, the photosynthetic response in LndAtm to lowered  $g_{1M}$  (lowered water cost) is generally negative (although much smaller in magnitude than the response to higher  $g_{1M}$  perturbations; cf. Figs. 3b&d, with a global average photosynthesis decrease of  $50 \text{ gC/m}^2/\text{year}$  for lower  $g_{1M}$ . There were large regions in which photosynthesis rates increased in the lower  $g_{1M}$  compared to the default  $g_{1M}$  experiment (e.g., over southeast Asia and the Sahel; Fig. 3d). The spatial pattern of change in photosynthesis due to lower  $g_{1M}$  is similar to the change in precipitation, suggesting a connection between the two (cf. Fig. 3d and Fig. S4h). However, water availability variables such as soil water stress and VPD do not share the same response pattern as photosynthesis (cf. Fig. 3d and Figs. S4f&g). Interestingly, the precipitation response pattern to low  $g_{1M}$  is also similar to that in response to higher  $\text{CO}_2$  reported in Kooperman et al. (2018), which is consistent since plant water cost per carbon gain generally decreases with higher  $\text{CO}_2$ .

In contrast to the high  $g_{1M}$  simulations, the photosynthetic response to lower  $g_{1M}$  is sensitive to land-atmosphere and dynamic vegetation feedbacks (cf. Figs. 3c&d), with some regions showing a response in opposite directions. Regions with the same direction of photosynthetic response between the LndOnly and LndAtm low  $g_{1M}$  simulations tend to have a greater response in the LndAtm simulation (cf. Figs. 3c&d and Fig S4g). In several regions, the sign of response of photosynthesis to low  $g_{1M}$  depends on whether the atmosphere and/or leaf area are allowed to change including in the Amazon, central North America (central NA), and boreal Canada (Fig. 3e). We discuss each of these three regions in further detail below.





**Figure 3.** Spatial difference plots of photosynthesis for high minus default  $g_{1M}$  (water cost) at (a) Land-Only-Fixed-Leaf (LndOnly) and (b) Land-Atmosphere (LndAtm) configurations and low minus default  $g_{1M}$  (water cost) at (c) Land-Only-Fixed-Leaf (LndOnly) and (d) Land-Atmosphere (LndAtm) configurations. The response to higher and lower  $g_{1M}$  are at different scales. Stippled grid cells represent differences that are not statistically significant. Statistical methods are detailed in Section 2.5. (e) A spatial plot showing the difference in the sign of the photosynthetic change in the Land-Only-Fixed-Leaf (LndOnly) and Land-Atmosphere (LndAtm) low minus default  $g_{1M}$  simulations. Colored grids indicate where the sign of the change in the Land-Atmosphere (LndAtm) simulation is opposite to that in the Land-Only-Fixed-Leaf (LndOnly) simulation and the color represents the direction of change.



**Figure 4.** Percentage differences of photosynthesis and variables that can influence photosynthesis between the low and default  $g_{1M}$  (water cost) simulations using the Land-Only-Fixed-Leaf (LndOnly) and Land-Atmosphere (LndAtm) configurations in the (a) Amazon, (c) central North America, and (e) boreal Canada. Bars with a green (\*) are not statistically different from zero. Statistical methods are detailed in Section 2.5. The expected photosynthetic response estimated from perturbed meteorology for temperature ( $\frac{\Delta GPP_T}{\Delta T_T} \delta T_{LndAtm}$ ; red bar) and VPD ( $\frac{\Delta GPP_{VPD}}{\Delta VPD_{VPD}} \delta VPD_{LndAtm}$ ; blue bar) in (b) the Amazon, (d) central NA, and (f) boreal Canada. Temperature includes both direct effects of warming and indirect effects of VPD. The absolute difference in photosynthesis due to the change in  $g_{1M}$  (low minus default) between the Land-Atmosphere (LndAtm) and Land-Only-Fixed-Leaf (LndOnly) configurations are shown in green ( $\Delta GPP_{LndAtm} - \Delta GPP_{LndOnly}$ ). Note that the y-axis is unique to each plot.

### 3.2.3 Regional responses to low $g_{1M}$

We examine how the regional response of photosynthesis to  $g_{1M}$  (water cost) differs between LndAtm and LndOnly in three focal regions; the Amazon, central NA, and boreal Canada.

In the Amazon, in response to lower  $g_{1M}$  (lower water cost), photosynthesis decreased in LndAtm but increased in LndOnly (cf. Figs. 3c&d; Table 2; Fig. 4a), indicating that conditions controlling photosynthesis are greatly affected by atmosphere and/or dynamic vegetation feedbacks. Transpiration in the Amazon decreased in both configurations as plants closed their stomata in response to lower  $g_{1M}$ . Temperature and VPD both increase when the atmosphere is allowed to dynamically respond in LndAtm, while in LndOnly the meteorological conditions are identical between all experiments, and thus there are no changes in temperature and VPD.

Decreases in transpiration cause increases in temperature (and an increase in VPD) and a reduction in clouds further increases temperature and VPD in the Amazon (Table 2). Under decreased evaporation, in this case transpiration, the warming effect of decreased cloud cover is typically larger than decreased latent cooling (Laguë et al., 2023). As in the case of the Amazon, central NA shows a decrease in photosynthesis with lower  $g_{1M}$  in LndAtm and an increase in LndOnly (Table 2; Fig. 4c). We also found warming due to decreased latent cooling central NA, and shortwave cloud feedbacks occurred in all three of our focal regions. The Amazon had the largest magnitude of temperature increase (2.72°C) compared to central NA (0.97°C) and boreal Canada (0.59°C), and we note that this temperature increase in the Amazon occurred on top of an already higher baseline temperature.

Over boreal Canada, photosynthesis increased in response to lower  $g_{1M}$  in LndAtm and decreased in LndOnly (opposite to the Amazon and central NA; Table 2; Fig. 4e). As in the other regions, the LndAtm low  $g_{1M}$  simulation had much greater increases in surface temperature and in VPD (Table 2) relative to the simulations with prescribed atmospheric conditions. The VPD increase in boreal Canada was smaller than in the Amazon, consistent with a smaller absolute temperature change (cf. Figs. 4a&e; Table 2).

We attribute the cause of the response of photosynthesis to temperature and VPD using our perturbed meteorology simulations. In both the Amazon and central NA we find an increase in temperature alone tended to slightly decrease photosynthesis while an increase in VPD alone drastically decreased photosynthesis. Thus, we attribute the increase in VPD as the cause of the decrease in photosynthesis in both the Amazon and central NA because the magnitude of photosynthetic response to VPD alone was similar to the change in photosynthesis that we found between LndOnly and LndAtm (Figs. 4b&d). In boreal Canada photosynthesis increases in response to elevated temperature alone and decreases in response to elevated VPD alone (Fig. 4f). However, even though the direction of change in photosynthesis is consistent with the higher temperatures in LndAtm, the magnitude attributable to higher temperatures is much smaller in boreal Canada relative to magnitude attributable to either temperature or VPD in the other regions that we analyzed.

### 3.3 Elevated atmospheric CO<sub>2</sub>

Under elevated CO<sub>2</sub>, we find that photosynthesis increases across the globe for all  $g_{1M}$  (water cost) simulations (Figs. 5a-c), with an increase in response to a doubling of preindustrial CO<sub>2</sub> of 66 PgC/year for default  $g_{1M}$ , 70 PgC/year for low  $g_{1M}$ , and 60 PgC/year for high  $g_{1M}$  (Figs. 5a-c, additional details of photosynthetic response to elevated CO<sub>2</sub> for the globe and the boreal, temperate, and tropical bands can be found in Table S2).

**Table 2.** Climate Variable Responses to low  $g_{1M}$  (low minus default  $g_{1M}$ )

Variable	Amazon				Central NA				Boreal Canada			
	Land-Only-Fixed-Leaf		Land-Atmosphere		Land-Only-Fixed-Leaf		Land-Atmosphere		Land-Only-Fixed-Leaf		Land-Atmosphere	
	unit	%	unit	%	unit	%	unit	%	unit	%	unit	%
Photosynthesis ( $\text{gC}/\text{m}^2/\text{yr}$ )	110*	5.7*	-859*	-43.9*	109*	9.8*	-116*	-11.0*	-22.6*	-3.8*	86.2*	15.8*
Sunlit leaf $g_s$ ( $\text{gH}_2\text{O}/\text{m}^2/\text{s}$ )	-0.77*	-39.5*	-1.12*	-60.2*	-0.55*	-24.5*	-0.78*	-37.9*	-0.36*	-20.6*	-0.28*	-15.7*
Transpiration ( $\text{W}/\text{m}^2$ )	-20.7*	-35.1*	-35.7*	-59.5*	-3.53*	-10.8*	-6.66*	-22.3*	-1.84*	-21.3*	0.15	2.1
Latent heat flux ( $\text{W}/\text{m}^2$ )	-14.4*	-15.1*	-21.6*	-22.4*	-1.86*	-3.7*	-4.81*	-10.1*	-1.56*	-6.3*	-0.05	-0.2
Sensible heat flux ( $\text{W}/\text{m}^2$ )	13.2*	31.8*	16.2*	39.8*	1.60*	5.6*	4.44*	15.5*	1.42*	7.6*	1.58*	8.2*
Soil water stress (unitless)	-0.40*	-89.1*	-0.49*	-124*	-0.11*	-13.3*	-0.03*	-2.7*	-0.01	-1.0	-0.01*	-1.6*
Soil liquid water (kg)	80.5*	8.8*	81.6*	9.0*	123*	18.7*	2.73	0.4	4.48	0.6	40.4*	5.6*
Surface temperature ( $^{\circ}\text{C}$ )	0.09	0.3	2.72*	10.2*	0.02	0.3	0.98*	11.0*	0.01	0.5	0.57*	32.5*
VPD (Pa)	-	-	674*	33.0*	-	-	127*	16.6*	-	-	28.0*	9.1*
Low cloud cover (fraction)	-	-	-0.07*	-39.9*	-	-	-0.04*	-15.3*	-	-	-0.02*	-3.7*
Incident solar radiation ( $\text{W}/\text{m}^2$ )	-	-	2.00*	0.9*	-	-	4.17*	2.4*	-	-	2.11*	1.8*
Total leaf area ( $\text{m}^2/\text{m}^2$ )	-	-	-2.07*	-53.3*	-	-	-0.38*	-16.7*	-	-	0.14*	10.2*

We represent the statistical significance of two comparisons, between simulations with different  $g_{1M}$  (\*), and between the two model configurations (bold).

A star (\*) indicates low minus default  $g_{1M}$  responses pass a test for statistical significance, where the null hypothesis is that there is no difference between the low  $g_{1M}$  and default  $g_{1M}$  simulations. **Bolded** values indicate where the differences between the Land-Only-Fixed-Leaf (LndOnly) and Land-Atmosphere (LndAtm) configurations for low minus default  $g_{1M}$  pass a test for statistical significance, where the null hypothesis tested is that there is no difference between these two sets of differences.

Generally we find that low  $g_{1M}$  increases photosynthesis further from default  $g_{1M}$ , and high  $g_{1M}$  perturbation moderates the increase in photosynthesis, although there are regions that do not follow this pattern (Figs. 5d&e). However, overall, the additional photosynthetic response to  $g_{1M}$  perturbations are small relative to the photosynthetic response to elevated  $\text{CO}_2$ . Even so, assumptions about stomatal function modify the total global photosynthetic response to a doubling of preindustrial  $\text{CO}_2$  by 6.4% for low  $g_{1M}$  and by -9.6% for high  $g_{1M}$  relative to default  $g_{1M}$ . At lower  $g_{1M}$ , photosynthesis increases relative to default  $g_{1M}$  in 58% of grid cells and decreases in 42% of grid cells. The change at higher  $g_{1M}$  is more spatially widespread, with increases relative to default  $g_{1M}$  in photosynthesis in only 27% of grid cells and decreases in 74% of grid cells.

We note that Australia has an absolute decrease in photosynthesis in response to elevated  $\text{CO}_2$  with lower  $g_{1M}$  contrary to the rest of the globe, and a larger relative change in response to  $g_{1M}$  (Fig. 5). We find that this can be explained by the substantial reduction in leaf area in response to lower  $g_{1M}$  (whether due to perturbations in  $g_{1M}$  or elevated  $\text{CO}_2$ ), with leaf area nearly reaching zero in the west and halving in the east with lower  $g_{1M}$  (see further discussion of leaf area decrease in Supplemental Text S2; Fig. S6).

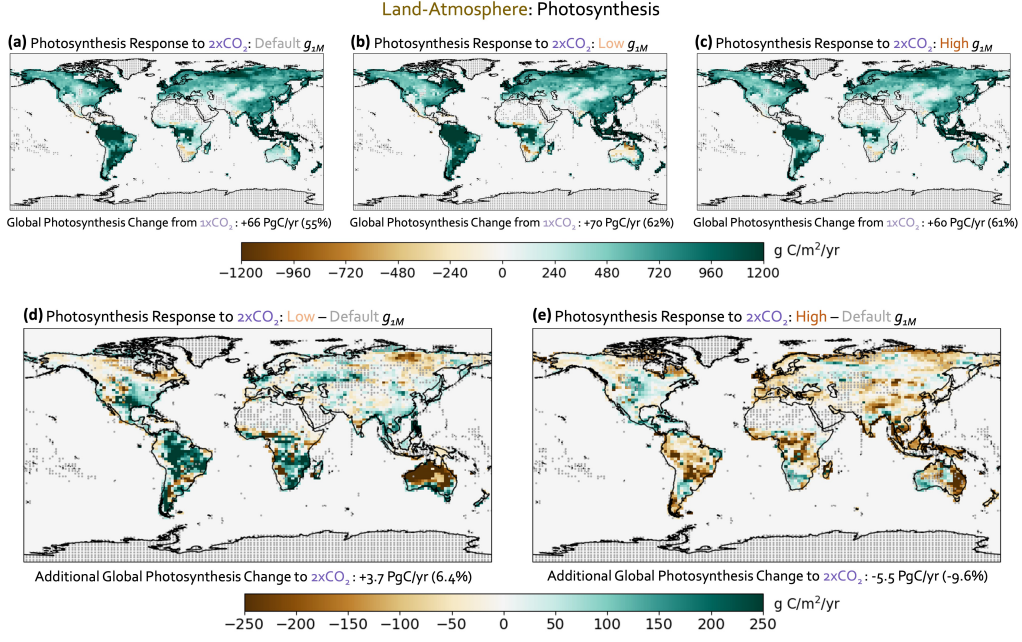
## 4 Discussion

### 4.1 Inclusion of a dynamic atmosphere evoked strong temperature and VPD responses that affected photosynthesis

Broadly, we expected photosynthesis to decrease with lower  $g_{1M}$  (lower water cost) as photosynthesis and stomatal conductance are tightly coupled, with both regulated by stomata and iteratively calculated in the model. Although we find some regions of decrease in photosynthesis we also find regions of increase (Figs. 3c&d). Not only was photosynthetic response to lower  $g_{1M}$  not consistent across regions, it was also not consistent across configurations of CESM2, flipping sign between increasing and decreasing photosynthetic response to the same change in  $g_{1M}$  depending on the the inclusion of a dynamic atmosphere and prognostic leaf area (Fig. 3e). The change in the sign of photosynthetic response to  $g_{1M}$  can be largely attributed to the inclusion of a dynamic atmosphere rather than prognostic leaf area (cf. Fig. 3e and Fig. S5).

To explain why photosynthesis shows a different direction of response to a decrease in  $g_{1M}$  when the atmosphere is allowed to dynamically respond (LndAtm compared to LndOnly), we explored four possible conjectures based on what we know about photosynthesis and its response to environmental factors. First, the low  $g_{1M}$  and default  $g_{1M}$  simulations could have differences in  $g_s$  in response to  $g_{1M}$  (conjecture 1; c1; Fig. 6b). Second, photosynthesis could be responding to plant soil water stress (conjecture 2; c2; Fig. 6c). Third, photosynthesis could be responding to a change in temperature which differs between LndAtm and LndOnly (conjecture 3; c3; Fig. 6d). Fourth, photosynthesis could be responding to atmospheric water stress (conjecture 4; c4; Fig. 6e). We note that given the coupled nature of the system, the four conjectures interact with each other (Fig. 6a). To evaluate these conjectures we focus on regions that had a change in the sign of photosynthetic response to  $g_{1M}$  between the LndAtm and LndOnly low  $g_{1M}$  simulations (Fig. 3e).

To start, there was a  $g_s$  decrease in response to lower  $g_{1M}$  perturbation in almost all regions for both the LndAtm and LndOnly simulations (Fig. S3b and Fig. S4b), which would on its own cause a decrease in photosynthesis, and thus changes in  $g_s$  (c1) alone cannot explain the difference in photosynthetic response between the two experimental groups (and hence model configurations). We note that the Tibetan Plateau region did not match the general global  $g_s$  response (Fig. S3b and Fig. S4b) because the C3 arctic grass PFT default  $g_{1M}$  used in CLM5 was lower than the low  $g_{1M}$  perturbation de-



**Figure 5.** Photosynthesis difference spatial plots of default  $g_{1M}$  (water cost) between  $1\times\text{CO}_2$  and  $2\times$  preindustrial atmospheric  $\text{CO}_2$  concentrations for (a) default, (b) low, and (c) high  $g_{1M}$  perturbations, where  $g_{1M}$  is constant for each comparison. Spatial difference plots showing the additional change in photosynthesis in response to a doubling of atmospheric  $\text{CO}_2$  in the Land-Atmosphere (LndAtm) configuration when the default  $g_{1M}$  is replaced by (d) low  $g_{1M}$  and (e) high  $g_{1M}$  (see Section 2.3.3 for comparison details). The additional change in photosynthesis is calculated by taking the difference of the photosynthetic response to  $g_{1M}$  perturbation at  $2\times\text{CO}_2$  and  $1\times\text{CO}_2$  (e.g.,  $2\times\text{CO}_2(\text{low} - \text{default } g_{1M}) - 1\times\text{CO}_2(\text{low} - \text{default } g_{1M})$ ). Note the different scale in *a-c* and *d-e*. Stippled grid cells represent differences that are not statistically significant. Grid cells are statistically significant if the photosynthetic response to  $g_{1M}$  perturbation at  $2\times\text{CO}_2$  is different from the photosynthetic response to  $g_{1M}$  perturbation at  $1\times\text{CO}_2$ . Statistical methods are detailed in Section 2.5.



rived from Lin et al. (2015) (Fig. 1a). The changes in soil water stress (c2), temperature (c3), and atmospheric water stress (c4) vary more across regions, so we discuss the response by region below.

#### 4.1.1 *VPD-driven photosynthesis decreased in the Amazon and central North America*

For simulations with a prescribed atmosphere (LndOnly), we found a photosynthetic increase in the Amazon and central NA in response to lower  $g_{1M}$  (lower water cost) which is most likely driven by a reduction in soil water stress (c2) because temperature (c3) and VPD (c4) did not change much with fixed atmospheric forcing (Fig. 4). During the Amazon dry season, the low  $g_{1M}$  simulation had similar  $g_s$  (c1) but lower soil water stress (c2) compared to the default  $g_{1M}$  simulation. This is due to a cumulative difference in transpiration rates allowing for soil water conservation that carries over into the dry season resulting in increased photosynthesis (Fig. S7). In central NA, photosynthesis increased during the growing season as reduced soil water stress (c2) outweighed the decrease in  $g_s$  (Fig. S7).

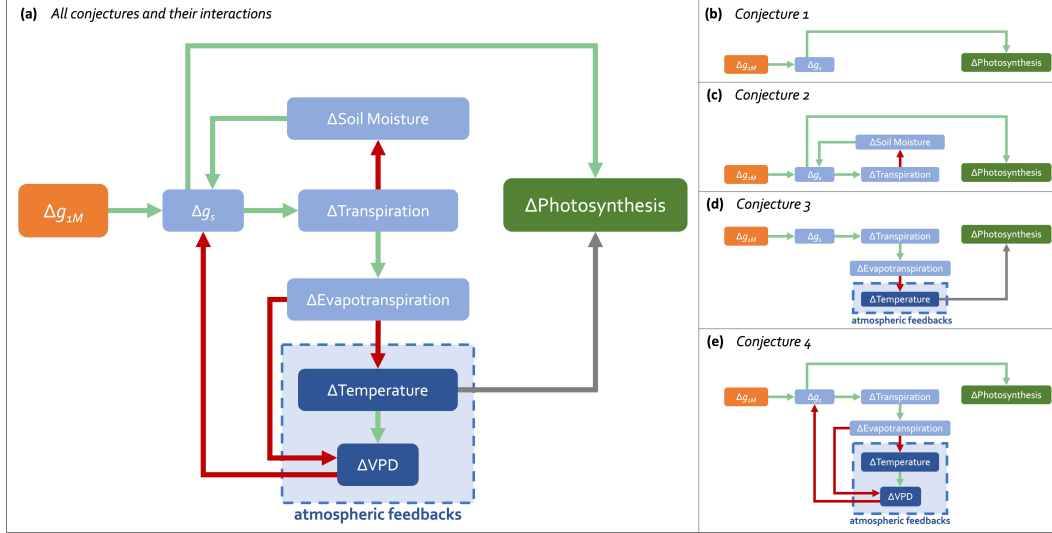
For simulations with a dynamic atmosphere and prognostic leaf area (LndAtm), we find that photosynthesis decreases. This can not be explained by soil water stress (c2), which is alleviated with lower  $g_{1M}$  in the Amazon and remains neutral in central NA. It is important to note that in the original formulation from Medlyn et al. (2011),  $g_{1M}$  was intended to dynamically respond to soil water stress (c2) but is static according to PFT within CLM5 due to limitations in soil–plant–atmosphere continuum representation (G. B. Bonan et al., 2014), however CLM5 does include a dynamic hydraulic conductance which includes soil, root, stem, and leaf water potentials that could address some of the limitations (Kennedy et al., 2019). This limitation implies that our results may not fully account the effects of soil water stress (c2) on photosynthesis.

The main differences between the response to lower  $g_{1M}$  in LndAtm and LndOnly are in the surface temperature (c3) and VPD (c4) responses. Temperature (c3) increased significantly in both the regions, which could potentially push plants beyond their thermal optima for photosynthesis (Yamori, Hikosaka, & Way, 2014; Figs. S3e & S4e). However, CLM5 includes a representation of photosynthetic acclimation (Lombardo et al., 2015) which reduces the negative impact of hot temperatures.

We attribute the photosynthetic decreases with a dynamic atmosphere primarily to a response to VPD (c4) as the magnitude of expected photosynthetic response to an increase in VPD alone explains the total signal (Figs. 4b&d) and is substantially larger than the response to temperature (c3) alone. The photosynthesis decrease in the Amazon is larger than in central NA, suggesting that plants in the Amazon are more sensitive to an increase in VPD (c4). This is consistent with prior modeling work showing that photosynthesis declines at high temperatures in tropical forests are mostly due to VPD effects rather than direct temperature effects in the land component of CESM2 (CLM5) (Zarakas, Swann, Koven, et al., 2024). In addition to VPD impacts on photosynthesis, recent observational and experimental methods found that photosynthesis decline at higher temperature can also be attributed to biochemical responses such as increases in mitochondrial respiration and photorespiration, Rubisco deactivation, and decreases in electron transport (Crous et al., 2024; Scafaro et al., 2023). Most land models lack full representation of these biochemical responses, so the projected decreases in photosynthesis at low  $g_{1M}$  may be underestimated.

#### 4.1.2 *Temperature increased photosynthesis in boreal Canada*

For boreal Canada we find a decrease in photosynthesis in response to lower  $g_{1M}$  (low water cost) in simulations with a prescribed atmosphere (LndOnly). In the LndOnly



**Figure 6.** Flowcharts illustrating simplified conceptual diagrams of the conjectures of how  $g_{1M}$  perturbation impacts photosynthesis. (a) shows all conjectures (c1-c4) and their interactions, while (b)-(d) focus on individual mechanisms:  $g_s$  (c1) in (b), soil moisture (c2) in (c), temperature (c3) in (d), and VPD (c4) in (e). Green arrows indicate positive relationships, red arrows negative relationships, and gray arrows relationships that depend on background climate. Changes in  $g_{1M}$  directly alter  $g_s$  which affects transpiration, sets off feedbacks through soil moisture (c2) and VPD (c4) that in turn influence  $g_s$ . Both  $g_s$  (c1) and temperature (c3) directly affect photosynthesis. Although leaf area is not shown in the diagram, changes in photosynthesis affect leaf area in prognostic leaf area simulations, which then directly feed back on to total photosynthesis and transpiration.

low  $g_{1M}$  simulation, we find support for the first conjecture as the decrease in  $g_s$  (c1) in boreal Canada had a greater effect on photosynthetic response than the small increase in soil water availability (c2) (Fig. 4e). When the atmosphere is allowed to respond to low  $g_{1M}$ , photosynthesis increased in boreal Canada. Soil water availability (c2), temperature (c3), and VPD (c4) all increase. If boreal plants were strongly influenced by higher VPD (c4) as they were in the Amazon and central NA, this would cause a decrease in photosynthesis. Yet photosynthesis increased, implying that plants were more sensitive to the direct effects of increases in temperature (c3) than in VPD (c4) and that temperatures remained primarily below rather than above thermal optimum (Fig. 4f). Although our direct attribution of the response of photosynthesis to an increase in temperature is smaller than the total increase in photosynthesis that we find, this could be explained by increased leaf area which is not included in our perturbed meteorology simulations (Fig. S4; Table 2).

The expected photosynthetic responses from temperature for all three regions suggest that the total effect of temperature (c3) on photosynthesis is influenced by the background climate. A low baseline temperature region, like boreal Canada, may have positive responses to temperature increases while a high baseline temperature region, like the Amazon and central NA, may have negative responses to temperature increases, through both direct temperature effects and effects of higher VPD, which are indirectly driven by elevated temperature.

## 4.2 Implications for choice of $g_{1M}$ in Earth system models

In CESM2, each PFT is assigned a single  $g_{1M}$  value, a practice which is common across similar models (G. Bonan, 2019; Sabot et al., 2022). Given that plants in the real world exhibit variation in  $g_{1M}$  (Lin et al., 2015), our results provide insight as to how and where Earth system models may be over or underestimating photosynthesis due to variation in  $g_{1M}$  in both the mean-state and in response to elevated  $\text{CO}_2$ .

Our simulated global photosynthesis values fall within that range of 83-172 PgC/year across the ensemble of 16 dynamic global vegetation models in the “Trends and drivers of regional scale sources and sinks of carbon dioxide” (TRENDY) project (Jung et al., 2020). However, our range of 99-120 PgC/year across perturbed  $g_{1M}$  highlights the potential magnitude of the impact of uncertainty in this one single aspect of stomatal function on photosynthesis in a single model. The fact that the difference between the high and low  $g_{1M}$  values spans a smaller range than than TRENDY models suggests many other factors also influence photosynthesis, however, we demonstrate that sensitivity to  $g_{1M}$  is substantial and is varies regionally.

Because  $g_s$  and photosynthesis are coupled at the leaf level (G. J. Collatz et al., 1991; Medlyn et al., 2011; Franks et al., 2017), our simplest expectation is that the two should change in the same direction. In response to higher  $g_{1M}$  (higher water cost),  $g_s$  is expected to increase, and thus in our simplest framework, photosynthesis is also expected to increase. Although  $g_s$  increased as expected with higher  $g_{1M}$ , photosynthesis substantially decreased across the globe (Figs. 3a&b) due to an increase in soil water stress. The resulting very low photosynthesis with higher  $g_{1M}$  suggests that the 95<sup>th</sup> percentile  $g_{1M}$  values are too high to produce reasonable photosynthesis in CESM2, which leads us to the hypothesis that they are not representative of plants generally (see further discussion below).

With lower  $g_{1M}$  (lower water cost),  $g_s$  is expected to decrease, and thus in our simplest framework photosynthesis is also expected to decrease. However, we found increases in photosynthesis in some regions and decreases in other regions (Sections 3.2.2 & 3.2.3; Figs. 3c&d), driven by varying plant responses to hotter temperatures that depend on the background climate. In hot regions like the Amazon, higher temperatures decrease photosynthesis, while in cold regions like boreal Canada higher temperatures increase photosynthesis. Thus, depending on the region, photosynthesis of plants with lower  $g_{1M}$  than that currently assumed in CESM2 could be either over or underestimated (see further discussion below.)

In our elevated  $\text{CO}_2$  simulations,  $g_{1M}$  modulates the sensitivity of photosynthesis increases to  $\text{CO}_2$  increases (Equation 1). We expect lower  $g_{1M}$  to increase sensitivity, enhancing the photosynthetic increase, and higher  $g_{1M}$  to reduce sensitivity, dampening the photosynthetic increase (Medlyn et al., 2011). Our simulations align with these expectations, suggesting that CESM2 may underestimate photosynthesis if  $g_{1M}$  is lower than assumed, and overestimate photosynthesis if  $g_{1M}$  is higher than assumed. This also has implications for the total land carbon sink under elevated  $\text{CO}_2$ , with lower  $g_{1M}$  tending to increase gross photosynthesis and land carbon sink, while higher  $g_{1M}$  would do the opposite and tend to decrease the land carbon sink, all else being equal. However, warmer temperatures can counteract increases in the land carbon sink by increasing plant respiration and ecosystem carbon loss. Additionally, a closely related version of CESM2 has been shown to overestimate leaf area, and thus photosynthesis, compared to satellite observations (Song et al., 2021). Therefore, we note the caveat that the photosynthesis increases in our elevated  $\text{CO}_2$  simulations may also be overestimated.

Our results quantify the potential impacts of varying  $g_{1M}$  on photosynthesis and identify regions where  $g_{1M}$  drives the largest changes. Specifically, we highlight the trop-

ics where perturbed  $g_{1M}$  results in significant and large decreases for photosynthesis compared to the default  $g_{1M}$  at preindustrial atmospheric  $\text{CO}_2$  concentrations (cf. Figs. 3b&d).

The LndAtm high  $g_{1M}$  simulation had substantial photosynthesis decreases in the tropics, where broadleaf evergreen trees are the only PFT. This PFT has a high  $g_{1M}$  perturbation that is double the default  $g_{1M}$  value, which is a larger perturbation compared to that of other PFTs (Fig. 1). We expect that individual plants with such a high  $g_{1M}$  would likely be drought-tolerant and be able to withstand a higher water cost for carbon gain. However, our simulations contradict this expectation with large decreases in photosynthesis for higher  $g_{1M}$ , driven by soil water stress. We suggest that the high  $g_{1M}$  values for the broadleaf evergreen tropical PFT are not compatible with CESM2 and thus we hypothesize that the values are not representative of typical plants in these regions. The Amazon also has similarly large photosynthetic decreases in the LndAtm low  $g_{1M}$  simulation, primarily driven by VPD increases, as discussed in Section 4.2.1. However, we cannot disentangle the sensitivity of the photosynthetic response to  $g_{1M}$  and to atmospheric feedbacks with our simulations.

Models differ in parameterizations, such as whether plant water stress is jointly determined by soil moisture and VPD, which can influence both the sensitivity of photosynthesis to  $g_{1M}$  and the relative importance of different drivers (Trugman et al., 2018; Trugman, 2022; Zarakas, Swann, Koven, et al., 2024). Despite these differences, we expect that most models would show qualitatively similar photosynthesis responses to those we observed in CESM2, where increasing  $g_{1M}$  past a certain threshold leads to decreases in photosynthesis. This would occur because changes in plant water use alter surface fluxes (Franks et al., 2024), changing VPD and temperature, which in turn influence photosynthesis through plant water stress. The general mechanism of land-atmosphere feedbacks on water stress are broadly represented across models, although the details would differ. Thus we hypothesize that the overall behavior should be expected in many models, while the specific threshold for this response will depend on how water stress is parameterized in each model.

### 4.3 Implications for tree-ring based observations

Our stomatal function perturbations through  $g_{1M}$  influence both  $g_s$  and photosynthesis, leading to changes in iWUE. In our simulations, iWUE increased with lower  $g_{1M}$  due to a decrease in  $g_s$ , while it decreased with higher  $g_{1M}$  due to an increase in  $g_s$  and a decrease in photosynthesis (Figs. S1-S4). If plants had higher or lower  $g_{1M}$  than what is currently assumed in CESM2, iWUE would be overestimated or underestimated, respectively. Because our findings relate changes in stomatal function to changes in stomatal conductance, photosynthesis, and iWUE in the context of a dynamic atmosphere, they can be used to help interpret tree-based isotopic observations (Saurer et al., 2014; Adams et al., 2020).

### 4.4 Model limitations in representing decoupling of $g_s$ and photosynthesis under high heat stress

Currently in CESM2, which uses the optimal stomatal conductance formulation (Medlyn et al., 2011), plants tend to decrease  $g_s$  under high temperatures and high VPD to reduce water loss through transpiration. However, some plant species have been observed to increase  $g_s$  under heat stress, presumably increasing transpiration for evaporative cooling to prevent thermal leaf death or as an unavoidable response to intense heat (Marchin et al., 2022). This plant response to high temperatures is currently not implemented in any Earth System models and decouples photosynthesis and  $g_s$  (Marchin et al., 2023). In the context of our results, our simulations could be underestimating plant transpiration under high temperatures and high VPD conditions, particularly for the low  $g_{1M}$  simulations. The greater water fluxes could lead to different atmospheric feedbacks,

potentially dampening the response of temperature and VPD increases. Additionally, the representation of leaf temperature is challenging in models and remains an unsolved problem. Errors in the estimation of leaf temperature relative to air temperatures impacts energy and water fluxes which could also potentially impact atmospheric feedbacks (Jiang et al., 2019; Hawkins et al., 2022). These atmospheric feedback changes can consequently influence the photosynthetic response.

## 5 Conclusions and Implications

Our research focused on how altering stomatal function, which governs water-carbon trade offs, affects photosynthesis. Overall we found that the answer was more complicated than one might initially guess, but that the response of photosynthesis can be explained by considering sensitivity to temperature and water availability. In particular, a dynamic atmosphere enabled the sign of photosynthetic response to reverse for low  $g_{1M}$  perturbation in the tropics and high latitudes. Other studies corroborate that choice of  $g_{1M}$  in land-atmosphere coupled simulations impacts the atmosphere (e.g., clouds and precipitation), underscoring the role of dynamic feedbacks between vegetation and climate (Franks et al., 2024). Thus, understanding how interactions between the land and the atmosphere are altered by land surface parameterizations is an important part of the process for model development and improvement.

Perturbed parameter ensembles (PPEs) have been used to quantify the impact of land parameter uncertainty and guide model calibration (McNeall et al., 2016; Dagon et al., 2020; Kennedy et al., 2025). PPEs reveal that parameters driving the most uncertainty can vary based on region and climate scenario (e.g., present-day and elevated  $\text{CO}_2$ ), highlighting a challenge of calibrating individual parameters within complex models (Kennedy et al., 2025). These PPE studies find that land parameter uncertainty can strongly impact land-to-atmosphere fluxes, however most land parameter PPEs have not included the effects of a dynamic atmosphere. Land parameter uncertainty has a substantial impact on the mean climate-state when the atmosphere is allowed to respond (Zarakas, Kennedy, et al., 2024). Our work underscores the need to evaluate the sensitivity to parameter perturbations in the context of a dynamic atmosphere. Only considering land parameter perturbations under prescribed atmospheric conditions risks generating opposite responses to those under dynamic atmospheric conditions as we have shown here.

Plants have a distribution of  $g_{1M}$  values (Lin et al., 2015). If this real-world distribution of  $g_{1M}$  is substantially different from the  $g_{1M}$  values embedded in Earth system models, we risk inaccurately modeling not only the mean-state photosynthesis but also its response to global change, particularly in the tropics. In this study we show that alternate representations of stomatal function, whether due to plant adaptation to climate change or land-use changes, can substantially alter modeled photosynthesis and its predicted responses to environmental change, including a hotter elevated  $\text{CO}_2$  world. We do not attempt to suggest an optimal  $g_{1M}$  value, but we emphasize that more accurately constraining  $g_{1M}$  is important for constraining regional carbon sink and that  $g_{1M}$  needs to be evaluated in the context of a coupled Earth system.

We recognize that  $g_{1M}$  can be represented in ways other than being assigned based on plant functional type. Franks et al. (2024) showed that mean annual precipitation based  $g_{1M}$  values in coupled CESM2 simulations can better match observations of photosynthesis derived with data products derived FLUXNET eddy covariance towers and satellite remote sensing (i.e., FLUXCOM). Additionally, using a soil-plant system model with the absence of atmospheric feedbacks, Y. Liu et al. (2021) showed that estimating  $g_{1M}$  with a model-data fusion method based on remote sensing data and assigning values by hydraulic functional type, rather than PFT, yields a better match with evapotranspiration observations from the microwave-based Atmosphere-Land Exchange Inverse (ALEXI)

algorithm. However, observations are still limited for representing  $g_{1M}$  with more granularity at global scales. Thus, measurements of stomatal function across a diversity of plant types, background climates, and CO<sub>2</sub> environments, ideally on mature plants in field settings and not just seedlings in greenhouses or growth chambers, would enable the community to build models that incorporate variability of plant traits and to more effectively use perturbed parameter ensembles to better quantify uncertainty in photosynthesis.

In our simulations we perturbed  $g_{1M}$  to its observational extremes (5<sup>th</sup> and 95<sup>th</sup> percentiles). Future simulations using a variety of other  $g_{1M}$  values (e.g., 25<sup>th</sup> and 75<sup>th</sup> percentiles) and incorporating different atmospheric feedbacks, including VPD and temperature feedbacks, could provide further insights to the sensitivity of photosynthesis to more moderate variation in  $g_{1M}$  and how it can affect global photosynthesis.

## 6 Open Research

The original data for this study are all available. Data used to perturb the stomatal slope parameter can be found at [https://figshare.com/articles/dataset/Optimal\\_stomatal\\_behaviour\\_around\\_the\\_world/1304289?file=1886204](https://figshare.com/articles/dataset/Optimal_stomatal_behaviour_around_the_world/1304289?file=1886204) (Lin et al., 2015). Model output from the  $g_{1M}$  (water cost) perturbation simulations are available the Dryad Digital Repository for this paper (DOI: 10.5061/dryad.c59zw3rj0; A. X. Liu et al., 2025). Model output from the perturbed meteorology simulations used in this paper is available in another Dryad Digital Repository (DOI: 10.5061/dryad.h44j0zpw1; Zarakas, Swann, & Battisti, 2024). Code used for the analysis in this paper is available at A. Liu (2025). CESM2 is open source and all code can be found on Github at <https://github.com/ESCOMP/CESM>.

## 7 Conflict of Interest Disclosure

The authors declare there are no conflicts of interest for this manuscript.

## Acknowledgments

AXL was supported by National Science Foundation Graduate Research Fellowship (DGE-2140004). CMZ was supported by the U.S. Department of Energy (DOE) Computational Science Graduate Fellowship (DE-SC0020347). The DOE Office of Biological and Environmental Research Regional and Global Model Analysis (RGMA) Program supported ALSS, AXL, CMZ, BB, CJS, LRH, MH, GJK, ASC, and AEC (DE-SC0021209). CDK acknowledges support by the DOE BER under contract DE-AC02-05Cc11231 through the RGMA Program (RUBISCO SFA) and the NGEE-Tropics project. This material is based upon work supported by the National Center for Atmospheric Research, which is a major facility sponsored by the NSF under Cooperative Agreement No. 1852977. We would like to acknowledge high-performance computing support from Cheyenne (doi:10.5065/D6RX99HX) and data storage resources provided by NCAR's Computational and Information Systems Laboratory, sponsored by the National Science Foundation. We thank all scientists, software engineers, and administrators who contributed to CESM2's development. We thank the editor, associate editor, and three reviewers for their constructive comments that have improved the clarity and content of our manuscript.

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1009 doi: 10.1111/GCB.17449



# Supporting Information for ”Atmospheric feedbacks reverse the sensitivity of modeled photosynthesis to stomatal function”

Amy X. Liu<sup>1</sup>, Claire M. Zarakas<sup>1</sup>, Benjamin G. Buchovecky<sup>1</sup>, Linnia R.

Hawkins<sup>2</sup>, Alana S. Cordak<sup>3</sup>, Ashley E. Cornish<sup>3</sup>, Marja Haagsma<sup>4</sup>, Gabriel

J. Kooperman<sup>3</sup>, Chris J. Still<sup>5</sup>, Charles D. Koven<sup>6</sup>, Alexander J. Turner<sup>1</sup>,

David S. Battisti<sup>1</sup>, James T. Randerson<sup>7</sup>, Forrest M. Hoffman<sup>8</sup>, Abigail L.S.

Swann<sup>1,9</sup>

<sup>1</sup>University of Washington, Seattle, Department of Atmospheric and Climate Science

<sup>2</sup>Columbia University, Department of Earth and Environmental Engineering

<sup>3</sup>University of Georgia, Department of Geography

<sup>4</sup>Oregon State University, Department of Biological and Ecological Engineering

<sup>5</sup>Oregon State University, Department of Forest Ecosystems and Society

<sup>6</sup>Lawrence Berkeley National Laboratory, Climate and Ecosystem Sciences Division

<sup>7</sup>University of California, Irvine, Department of Earth System Science

<sup>8</sup>Oak Ridge National Laboratory

<sup>9</sup>University of Washington, Seattle, Department of Biology

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1. Text S1 and S2
2. Figures S1 to S7
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### Text S1. Perturbed meteorology simulation calculations

For each perturbed meteorology simulation, we calculated the expected response of photosynthesis ( $\delta GPP_{expected}$ ) to the change in temperature or VPD due to  $g_{1M}$  perturbation. We calculated the expected response of photosynthesis to a single meteorological perturbation as follows:

$$\Delta GPP_{met\ Var} = GPP_{perturb\ met\ Var} - GPP_{control\ met} , \quad (1a)$$

$$\Delta Var_{met\ Var} = Var_{perturb\ met\ Var} - Var_{control\ met} , \quad (1b)$$

$$\Delta Var_{LndAtm} = Var_{LndAtm\ perturb\ g_{1M}} - Var_{LndAtm\ default\ g_{1M}} , \quad (1c)$$

$$\delta GPP_{expected} = \frac{\Delta GPP_{met\ Var}}{\Delta Var_{met\ Var}} \times \Delta Var_{LndAtm} , \quad (1d)$$

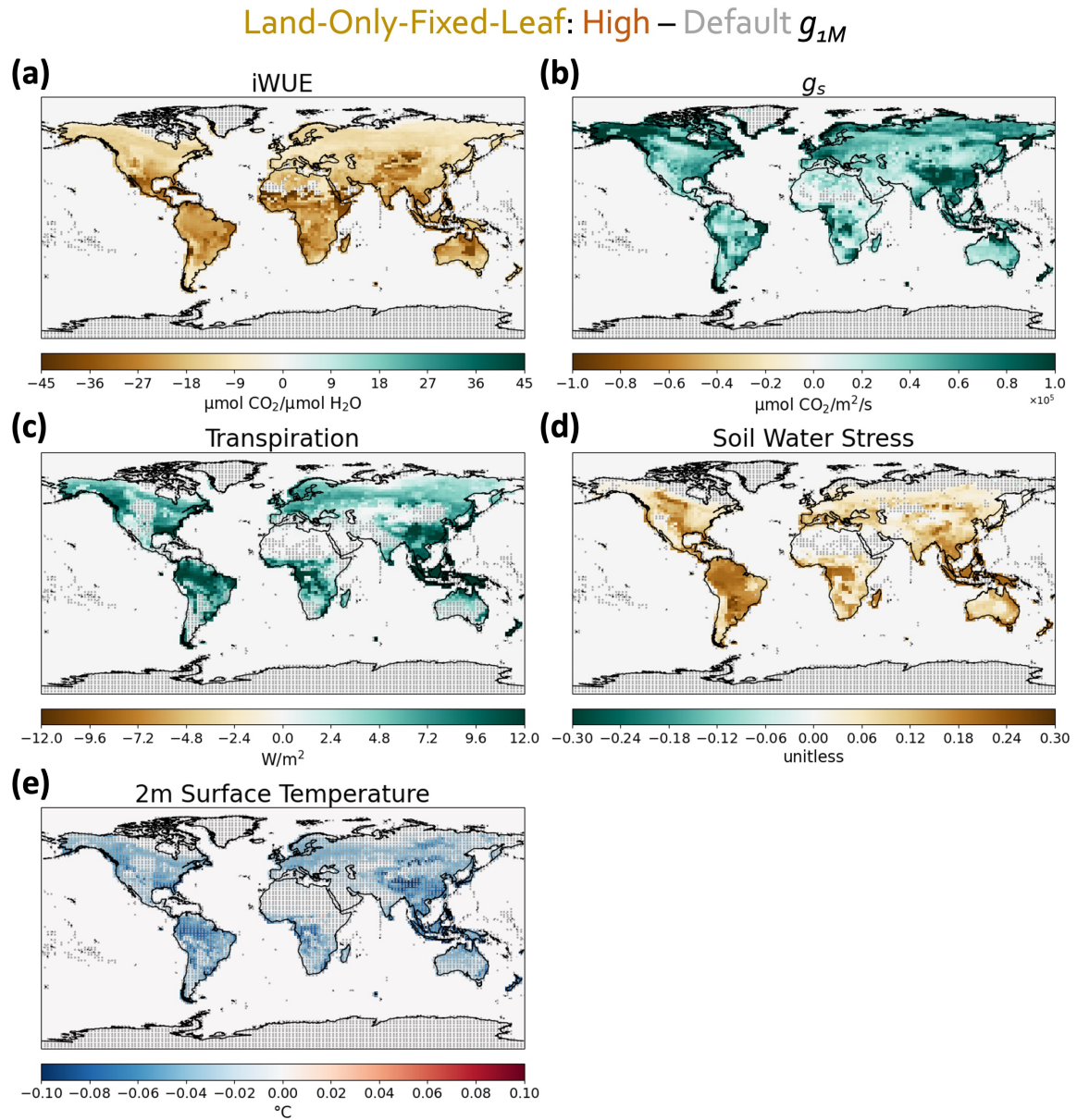
where  $Var$  is either temperature or VPD. Since the LndOnly simulations do not have changes in bottom of the atmosphere temperature or vapor pressure deficit (VPD), we did not include them in this part of the analysis. The first two equations (Eq. 1a&b) were calculated using the default values for  $g_{1M}$  and the “perturb met Var” refers to perturbed meteorology simulations.

### Text S2. Reasons why leaf area decreases in Australia in response to lower $g_{1M}$ at elevated CO<sub>2</sub>

In the main text, we attribute large photosynthesis decrease at low  $g_{1M}$  (water cost) to plants decreasing their leaf area. We hypothesize two reasons for the the decrease in leaf area below.

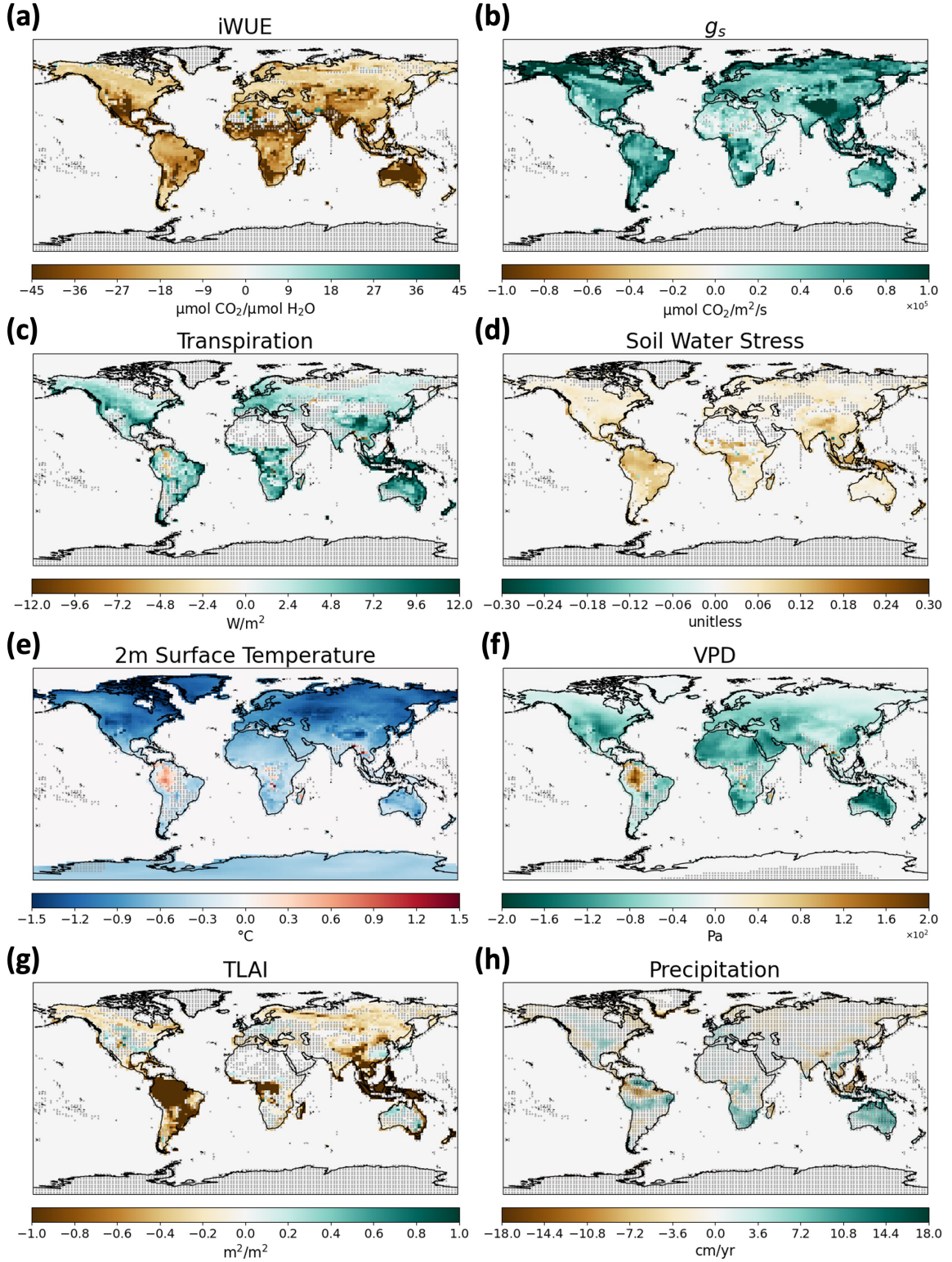
The first reason why leaf area decreases could be due to plants overheating. Since we were perturbing a low  $g_{1M}$ , plant stomata were forced to close more, which decreased

transpiration. This was followed by a decrease in latent heat flux and water vapor in the air, contributing heat and dryness to an atmosphere already warmed from the increase in CO<sub>2</sub>. In the real world plants transpire to regulate temperatures, but in model world that function is not implemented, so our plants in Australia could not cool down and may have decreased leaf area due to overheat. The second reason for leaf area reductions could be carbon starvation from stomatal closure. We already forced stomata close to some degree with our low  $g_{1M}$  perturbation, which could be amplified by an increase in atmospheric water stress due to an increase in VPD from decreased transpiration. If plants closed their stomata too much, they would not be able to diffuse in enough CO<sub>2</sub> for photosynthesis to upkeep its leaves and starve, hence the term carbon starvation.



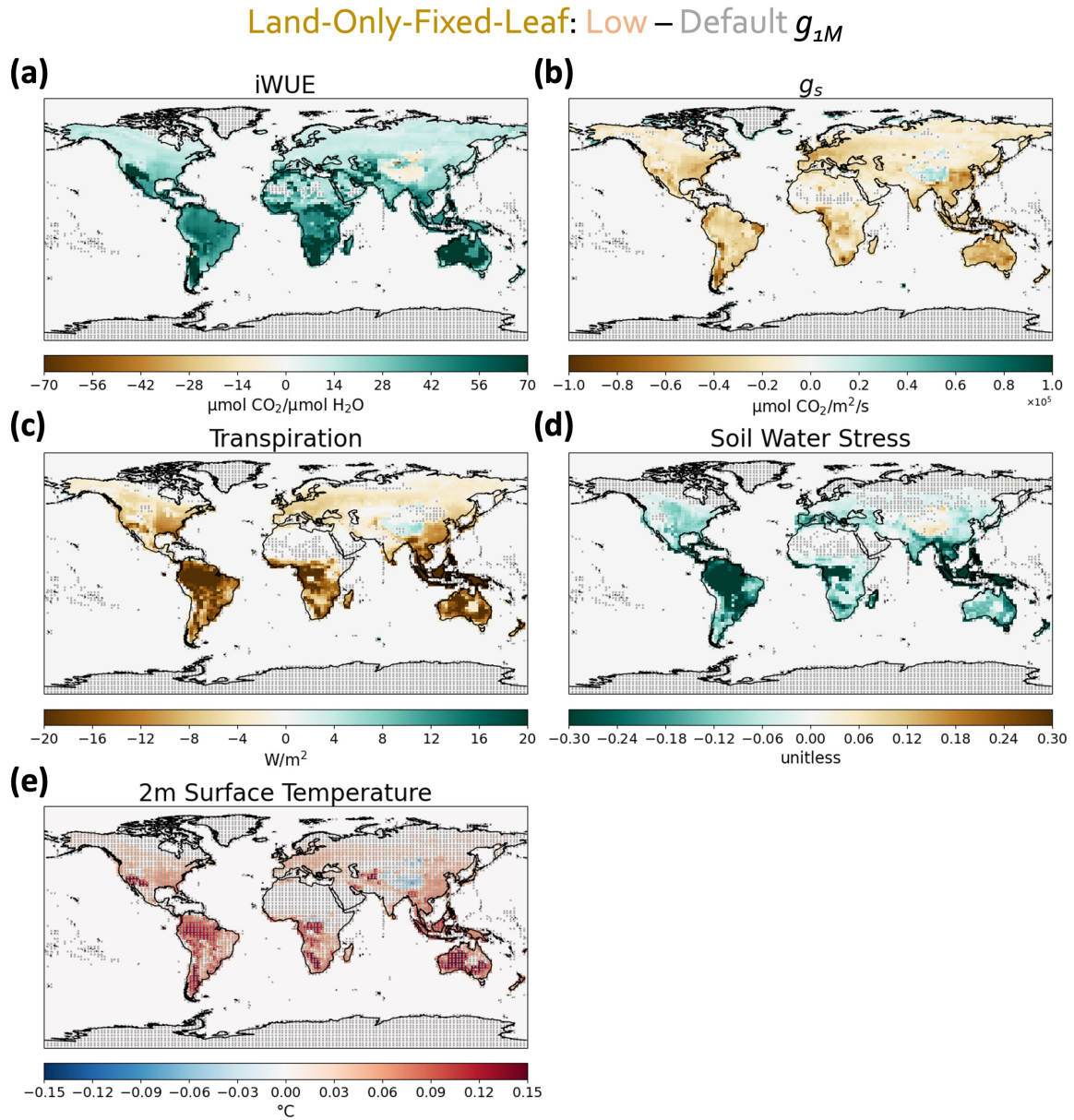
**Figure S1.** Spatial difference plots of (a) intrinsic water use efficiency (iWUE;  $\frac{\text{photosynthesis}}{g_s}$ ), (b) stomatal conductance ( $g_s$ ), (c) transpiration, (d) soil water stress, (e) surface temperature for high minus default  $g_{1M}$  at Land-Only-Fixed-Leaf (LndOnly) configuration. Stippled grid cells represent differences that are not statistically significant. Statistical methods are detailed in Section 2.5.

### Land-Atmosphere: High – Default $g_{1M}$



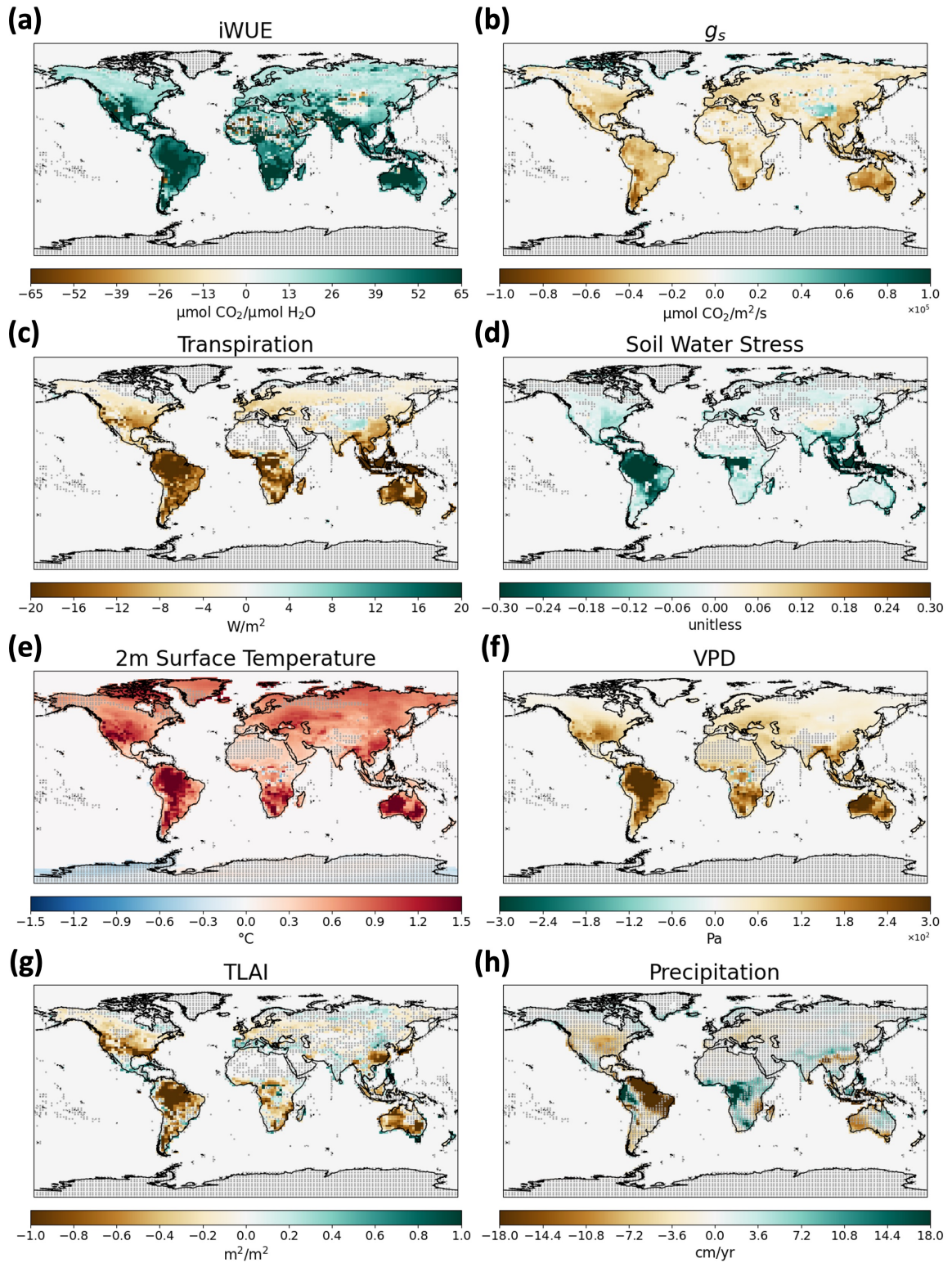
**Figure S2.** Spatial difference plots of (a) intrinsic water use efficiency (iWUE;  $\frac{\text{photosynthesis}}{g_s}$ ), (b) stomatal conductance ( $g_s$ ), (c) transpiration, (d) soil water stress, (e) surface temperature, (f) vapor pressure deficit, and (g) total leaf area for high minus default  $g_{1M}$  for the Land-Atmosphere (LndAtm) configuration. Stippled grid cells represent differences that are not statistically significant. Statistical methods are detailed in Section 2.5.



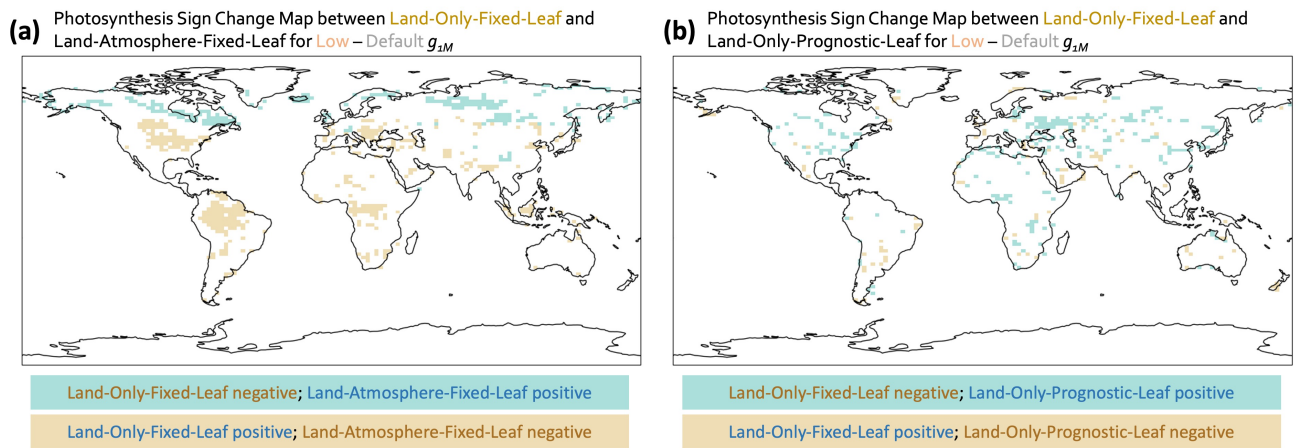


**Figure S3.** Spatial difference plots of (a) intrinsic water use efficiency (iWUE;  $\frac{\text{photosynthesis}}{g_s}$ ), (b) stomatal conductance ( $g_s$ ), (c) transpiration, (d) soil water stress, (e) surface temperature for low minus default  $g_{1M}$  for the Land-Only-Fixed-Leaf (LndOnly) configuration. Stippled grid cells represent differences that are not statistically significant. Statistical methods are detailed in Section 2.5.

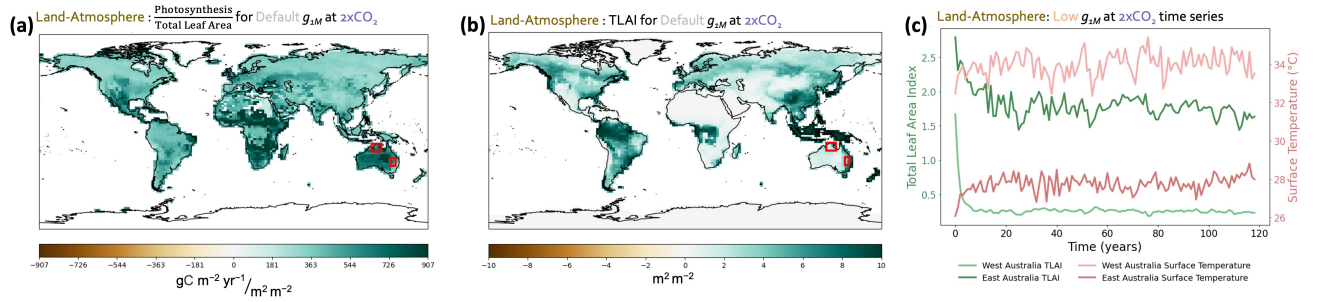
# Land-Atmosphere: Low – Default $g_{1M}$



**Figure S4.** Spatial difference plots of (a) intrinsic water use efficiency (iWUE;  $\frac{\text{photosynthesis}}{g_s}$ ), (b) stomatal conductance ( $g_s$ ), (c) transpiration, (d) soil water stress, (e) surface temperature, (f) vapor pressure deficit, and (g) total leaf area for low minus default  $g_{1M}$  for the Land-Atmosphere (LndAtm) configuration. Stippled grid cells represent differences that are not statistically significant. Statistical methods are detailed in Section 2.5.



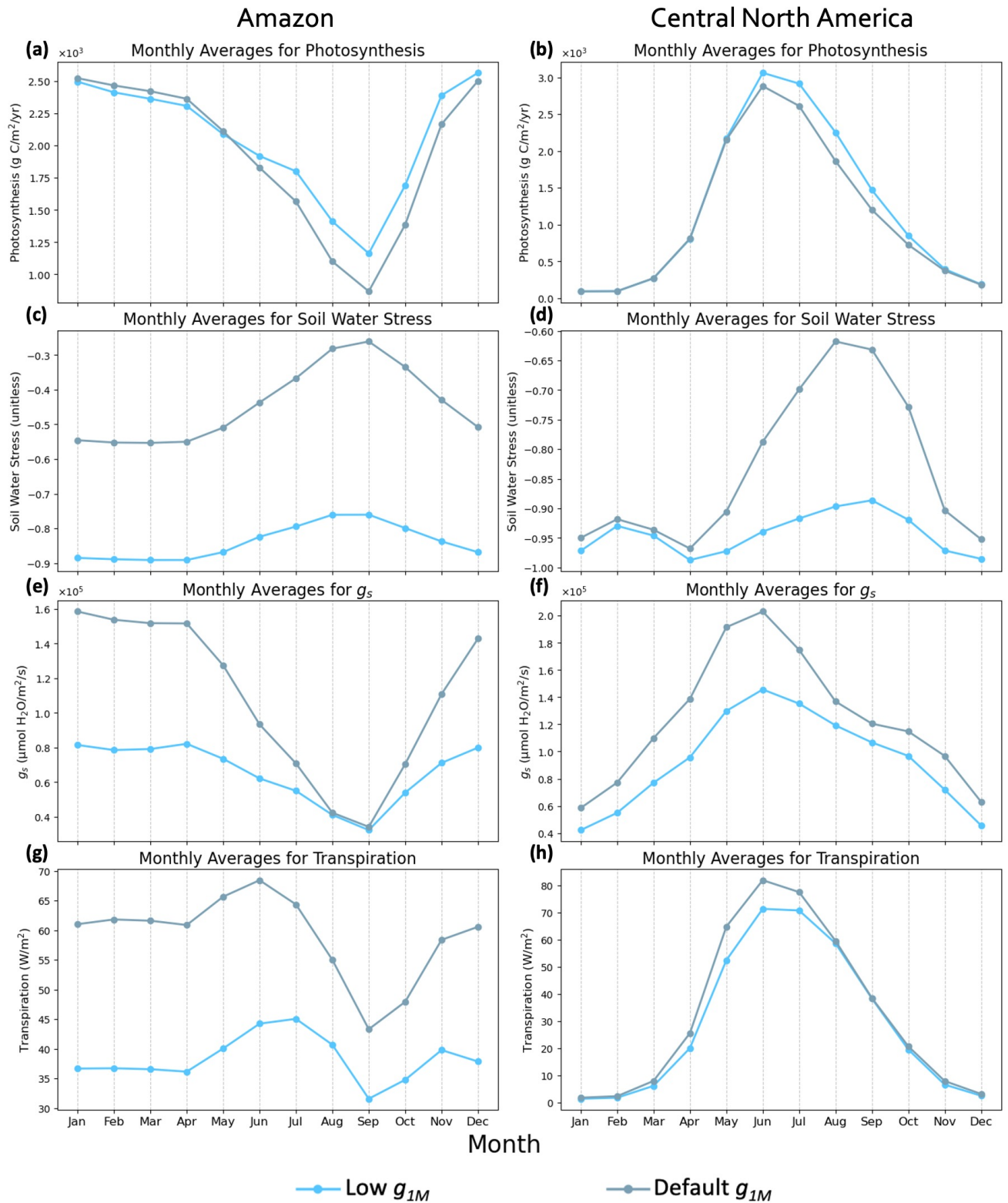
**Figure S5.** Spatial plots showing the difference in the sign of the photosynthetic change in the Land-Only-Fixed-Leaf (LndOnly) low minus default  $g_{1M}$  simulations and low minus default  $g_{1M}$  simulations for configurations that have either (a) the inclusion of a dynamic atmosphere (Land-Atmosphere-Fixed-Leaf) or (b) a prognostic leaf area (Land-Only-Prognostic-Leaf). Refer to Table S1 for configuration details. Colored grids indicate where the sign of the change in the Land-Atmosphere-Fixed-Leaf or Land-Only-Prognostic-Leaf simulations is opposite to that in the Land-Only-Fixed-Leaf (LndOnly) simulation and the color represents the direction of change.



**Figure S6.** (a) Global spatial plot of total photosynthesis normalized by total leaf area index (TLAI) at each grid cell for the Land-Atmosphere (LndAtm) default  $g_{1M}$  simulation at  $2\times$  preindustrial  $\text{CO}_2$ . (b) Global spatial plot of TLAI for the Land-Atmosphere (LndAtm) default  $g_{1M}$  simulation at  $2\times$  preindustrial  $\text{CO}_2$ . (c) Time series of TLAI and surface temperature for west and east Australia. The time series data was from pulled from the red boxes drawn in (a) and (b).



## Land-Only-Fixed-Leaf: Variables by Month



**Figure S7.** Averages of (a&b) photosynthesis, (c&d) soil water stress, (e&f)  $g_s$ , and (g&h) transpiration by month to show the seasonal cycle for Land-Only-Fixed-Leaf (LndOnly) default (grey line) and low  $g_{1M}$  (blue line) in the Amazon (left column) and central NA (right column). A more negative soil water stress corresponds to less soil water stress.

**Table S1.** Summary of Additional Simulations at 1x preindustrial CO<sub>2</sub> (284.7 ppm).

Simulation Name	Atmosphere	Leaf Area	$g_{1M}$ (Water Cost)
Land-Atmosphere-Fixed-Leaf low $g_{1M}$	dynamic	prescribed	low
Land-Atmosphere-Fixed-Leaf default $g_{1M}$			default
Land-Only-Prognostic-Leaf low $g_{1M}$	prescribed	prognostic	low
Land-Only-Prognostic-Leaf default $g_{1M}$			default

<sup>a</sup> Additional simulations used to attribute the change in sign of photosynthetic response

between the Land-Atmosphere (LndAtm) and Land-Only-Fixed-Leaf (LndOnly) configurations to the inclusion of a dynamic atmosphere and a prognostic leaf area (Fig. S5).

**Table S2.** Photosynthetic Response (PgC/yr) to elevated CO<sub>2</sub> at different  $g_{1M}$  assumptions.

Region	Latitude Range	$g_{1M}$ (Water Cost)	Starting PgC/yr	Ending PgC/yr	% Change
Global	0-90°N and °S	default	120	185	54.6
		low	112	182	61.8
		high	99	159	61.0
Boreal	50-60°N and °S	default	1.7	2.9	75.9
		low	1.6	2.9	77.4
		high	1.5	2.8	79.3
Temperate	23.5-50°N and °S (excludes boundary values)	default	15	22	44.9
		low	14	21	50.2
		high	14	20	46.2
Tropical	0-23.5°N and °S	default	18	26	45.3
		low	17	26	55.4
		high	13	21	55.4

<sup>a</sup> Photosynthetic response (PgC/yr) for 2x minus 1x preindustrial CO<sub>2</sub> at default, low, and high  $g_{1M}$  for different latitude belts (Figs. 4a-c). Photosynthesis values are rounded to either the nearest whole number or two significant figures, whichever is more precise, and percentage changes are rounded to one decimal place.